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STUDIES ON THE PHYSIOLOGY OF SCLEROTINIA CINEREA (BON.) WOR.

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

BY

JAMES LEWIS SEAL

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

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COCONUT BUD ROT IN FLORIDA

By James L. Seal

Technical Bulletin

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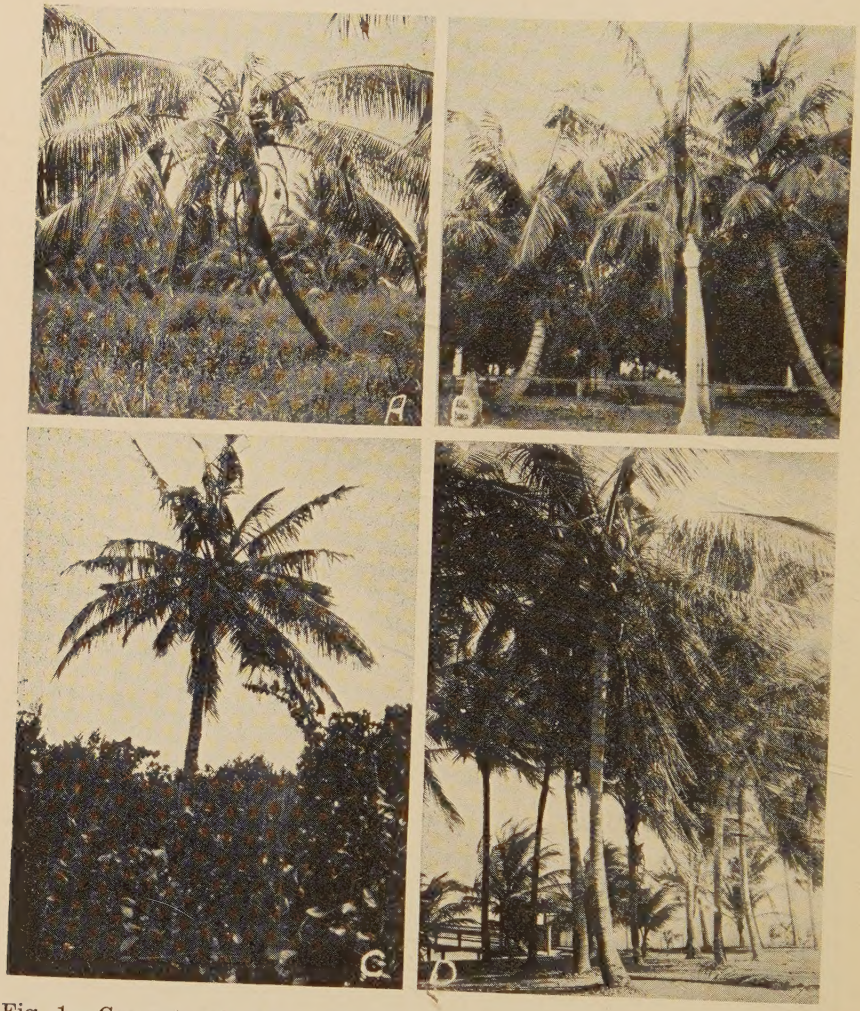

Fig. 1.—Coconut palms naturally infected with bud rot. In A, B, and C the buds are entirely missing, while in D the bud may be seen hanging from the top of the trunk.

COCONUT BUD ROT IN FLORIDA[1]

By JAMES L. SEAL[2]

INTRODUCTION

The most destructive disease of the coconut palm *(Cocos nucifera* Linn.) is bud rot. This disease is co-extensive with the palm, which, in general, may be found encircling the earth in a belt 1,500 miles north and south of the equator. Bud rot has been known for about a century, and the results of numerous researches on the disease have been published. In these various works, the authors do not agree upon a specific causal organism, as they suspect several species of *Phytophthora.* The work reported in this paper was undertaken with the view of establishing the relationship of the various so-called species of *Phytophthora* attacking the coconut palm.

DISTRIBUTION AND ECONOMIC IMPORTANCE

The coconut palm *(Cocos nucifera* Linn.) is found in all tropical countries within a belt of about 1,500 miles north and south of the equator. The origin of the coconut palm, according to Cook *(11)*,[3] seems to be Central America, as it is there that the greatest number of genera and species of the COCACEAE are found. Bud rot is practically co-extensive with its host and was reported from Cayman Island as early as 1834. Since then the disease has been reported from all the countries that grow the palm. From Florida there have been fragmentary reports for the past 30 years, but it was not until January, 1924, that a definite causal organism was found associated with the disease. At that time, Dr. G. F. Weber isolated an organism from a bud rotted palm growing in the vicinity of Miami. He considered the organism to be *Phytophthora faberi,* as described by Reinking *(28).* Since the above date the organism has been found generally distributed over the southeastern third of the state;

---

[1]This work was done in Florida while the writer was employed by the State Plant Board. The work was done under the supervision of Dr. O. F. Burger, to whom the writer wishes to acknowledge his indebtedness for encouragement and helpful criticism during the progress of the work. The writer also wishes to express his indebtedness to Drs. E. C. Stakman and M. N. Levine, for assistance in analyzing and presenting the material.

[2]A thesis submitted to the Faculty of the Graduate School of The University of Minnesota by James Lewis Seal in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

[3]Numbers in parentheses (italic) refer to "Literature Cited" in the back of this bulletin.

extending from south of Miami to Ft. Pierce, a total distance of about 140 miles along the coast. The great centers of palm

Fig. 2.—Coconut palms naturally infected by bud rot. A—Young palm with the diseased bud hanging from the top of the trunk. B—Bearing palm with the central column in process of falling from the tree. C—Row of old coconut palms interplanted with young plants, with both showing considerable bud rot. D—Young palms showing bud rot.

growing are around Miami and Palm Beach and it is here that the disease is most prevalent.

In Florida the coconut palm does not play the economic role that it does in many other parts of the world, but it does have considerable commercial value as an ornamental plant, as it is used very extensively in plantings in the southeastern section of the state, and, in 1925, had a commercial value of approximately $3,000,000. At present there are some 200,000 bearing trees and 2,000,000 or more nursery plants and young trees in the state. The plants are usually grown from the nuts by placing them in nursery formation, i. e. 2 to 3 feet apart in rows 3

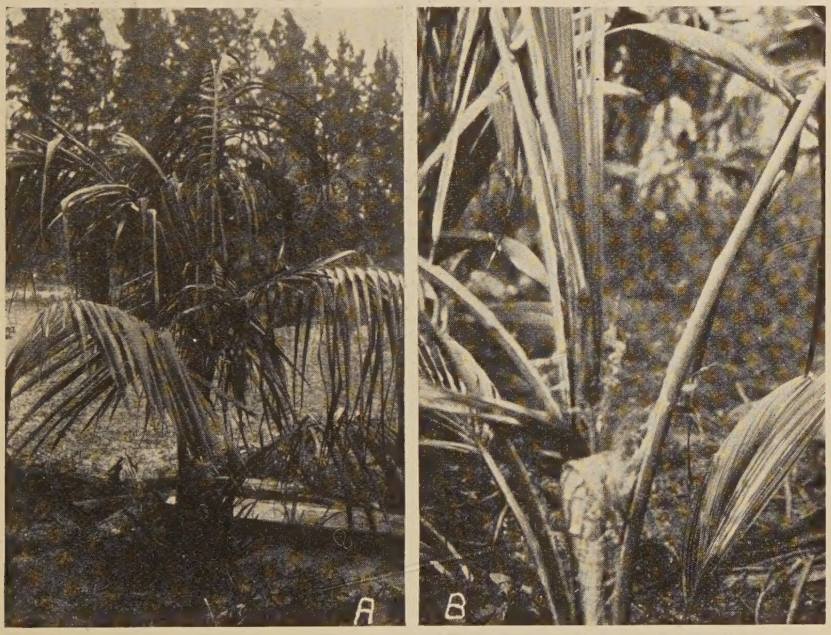

Fig. 3.—Two three-year-old nursery trees showing bud rot in different stages of development. A—Plant showing an early stage of the disease. B—Plant showing advanced stage of the disease.

to 5 feet wide. Under such conditions the plants are grown crowded for a period of two to five years. As the plants grow older they are usually thinned by removing every other plant. These nurseries are generally located on low peat soil where the plants make a very rapid growth, but nevertheless, they are usually inundated by water one or more times each year. It is in these nurseries that bud rot takes its greatest toll, but it is

not limited to palms on low ground, as bud rot has been found on many palms growing on high dry soil. Up to the present, some 75,000 diseased plants have been destroyed.

SYMPTOMS

The most noticeable symptom of bud rot is the dying and dropping of the bud during the later stages of the disease. The earlier stages of the disease may be recognized by one of three distinct symptoms: first, a spotting of the unrolling leaves,

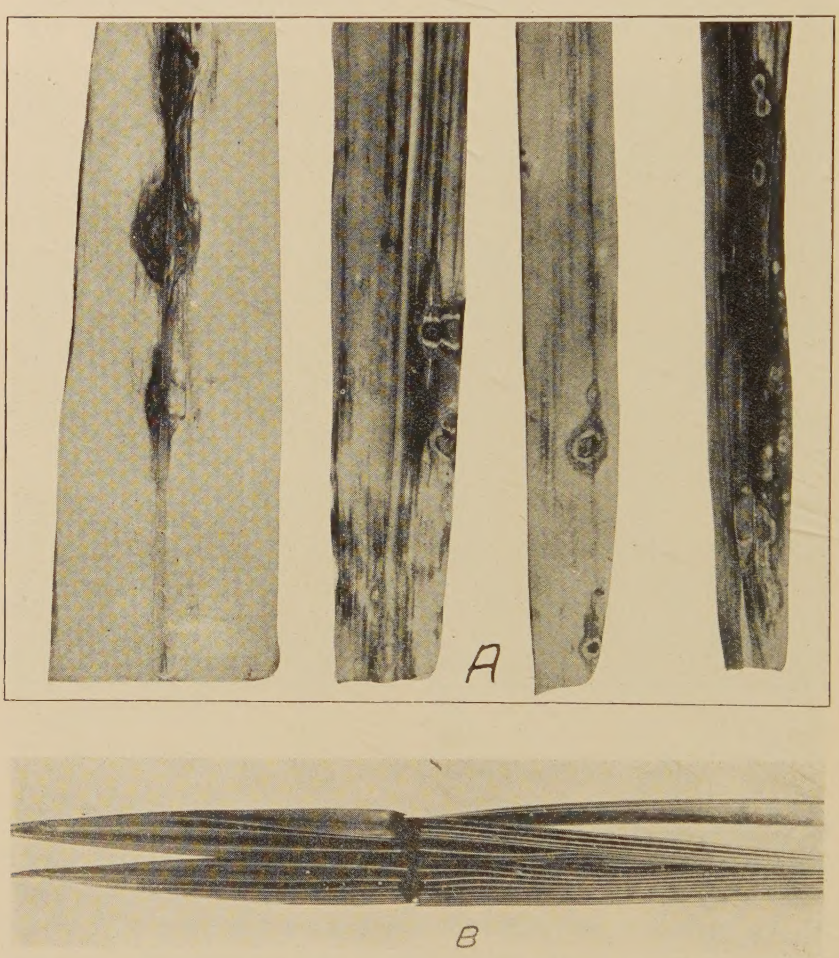

Fig. 4.—Two types of leaf injury often noted in inoculated plants. A—Spotting of the pinnae. B—Bud of young plant showing spotting across all the pinnae.

which may either be confined to a few of the leaflets or extend across all of a given leaf or, in some instances, several leaves; second, a blotching or killing of a few or many of the leaflets before they emerge from the sheath; and third, a sickly yellowish appearance of the leaves, with or without spotting, as they emerge from the sheath. In the first case the plant may recover from the disease readily, as the fungus has not attacked the primordal tissues; but in the second case the plant usually suc-

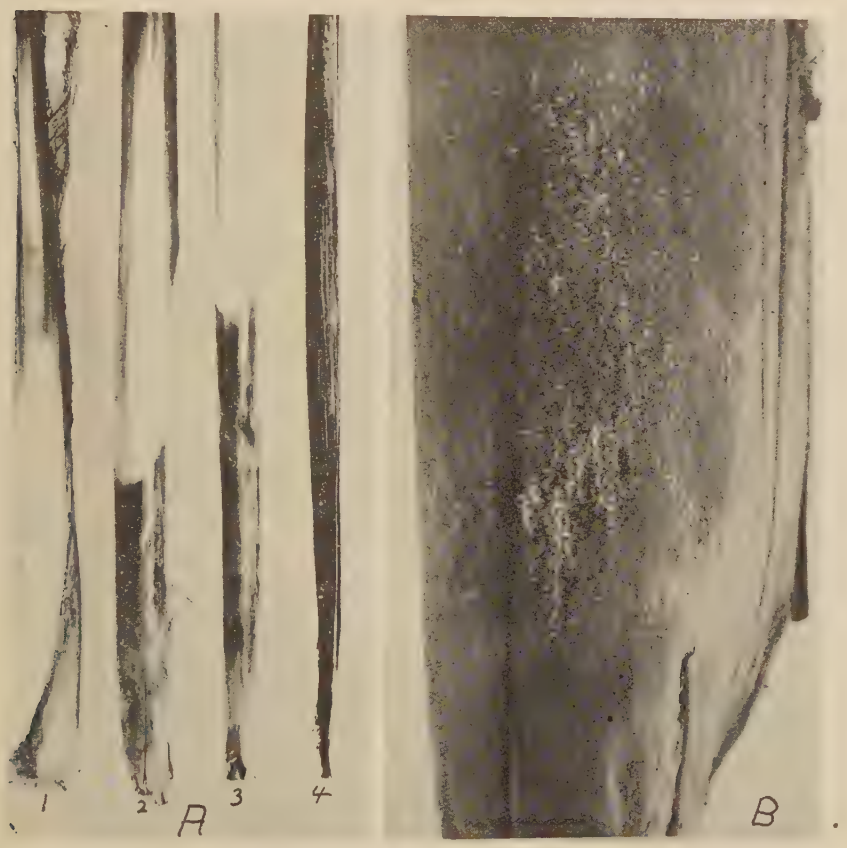

Fig. 5.—Bases of leaves from a naturally infected palm. A—Four leaf bases from a bud rotted palm arranged from right to left as they appeared around the bud. B—Enlarged view of No. 3 in A, showing tufts of mycelium on the tissues.

cumbs to the attack of the fungus, as every succeeding leaf is usually infected and it is usually only a short time until the fungus reaches the primordal tissues. In the third case the pri-

mordal tissues are infected at the time the symptom is noted, and it is only a matter of a few days until the bud dies. The plant may remain alive for some time but it eventually dies as the older leaves are killed. In case a tree is bearing at the time it is attacked, the young nuts readily drop, while the older ones remain until mature. In the first stages of the disease the bud may easily be pulled from the plant, and the young meristematic tissues are usually in a gelatinous mass that extends up the petiole into tissues having a bluish or steel gray color, then into a water soaked area, and finally into the white or creamy yellow healthy tissues. In some cases there is a very distinct brown line of demarcation between the diseased and the healthy tissues. The firmer diseased tissues are frequently covered with fungal hyphae, sometimes bearing chlamydospores but rarely ever bearing conidia. The rotted tissues usually have a very repulsive hog pen odor.[4]

CAUSE OF THE DISEASE

In 1907 Butler *(6)* reported that a parasitic Phytophthora had been found in the bud of Palmyra palm *(Borassus flabellifer* Linn.), Coconut palm *(Cocos nucifera* Linn.), and possibly in the Areca palm *(Areca catechu* Linn.). He later concluded *(7)* that this organism was a species of Pythium and called it *P. palmivorum* Butler; but, still later, upon receiving a culture of an organism isolated by Ashby from coconut palm in Jamaica, he concluded that the correct name of the organism was *Phytophthora palmivora* Butler *(9)*. Coleman *(10)* in 1910 published the results of his researches on the organism attacking the Betel-nut palm and concluded that it was distinct from previously described organisms. He named it *Phytophthora omnivora* var. *arecae* n. sp. Shaw & Sundararaman *(31)*, Sundararaman *(35)*, and MacRae *(23)*, all working in India, have confirmed Butler's work and agree that *Phytophthora palmivora* Butler is the causative agent of bud rot in the various species of palms in India. Johnston *(17)*, from extensive researches on coconut bud rot in Cuba, reported in 1912 that *Bacillus coli*

[4]The symptoms as reported for coconut bud rot in Florida are essentially the same as those reported by Ashby *(2)* in Jamaica, Reinking *(28)* in the Philippines, and Tucker *(36)* in Porto Rico. The outstanding difference between the symptoms as described elsewhere and those in Florida is the bluish or steel gray color of the diseased tissues which has been noted frequently in specimens collected in the early stages of the disease in Florida.

(Ehrlich) Migula, or an organism practically identical with it, was the causal pathogene. Working in Jamaica, Ashby *(1)*, in 1915, described the coconut bud rot as reported by Johnston but, in addition, found a Phytophthora-like organism associated with the bacteria in producing the disease. In 1920 Ashby concluded that two different species of Phytophthora were involved. He stated that one, *P. palmivora*, caused a bud rot, and the second, *P. parasitica* Dastur, caused a leaf stalk rot. He also stated that

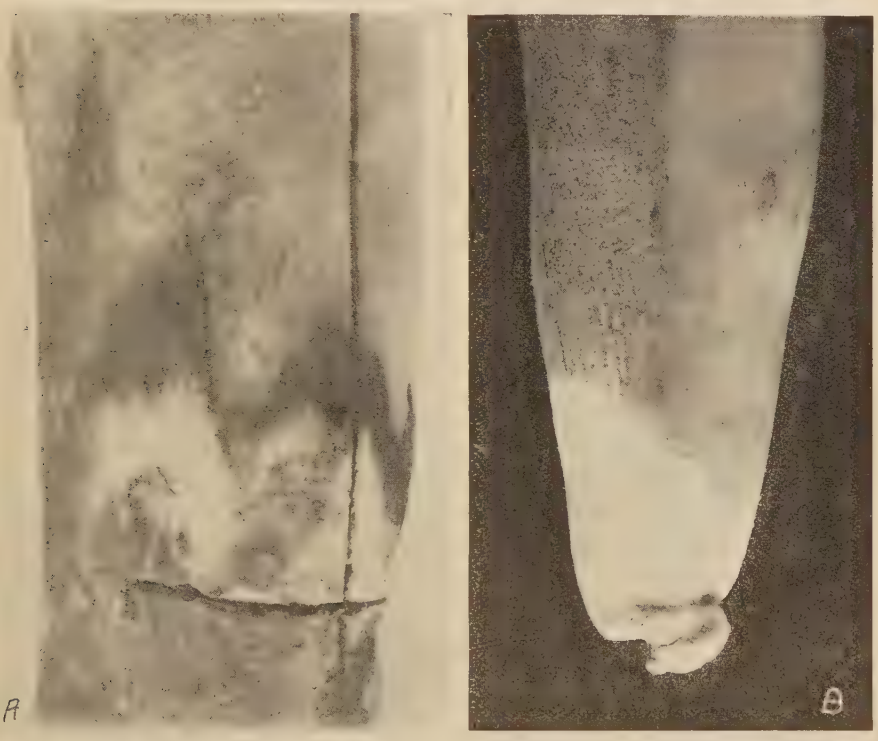

Fig. 6.—Buds of nursery palms in the early stages of bud rot, showing felts of mycelium on their basal parts. Lines of demarcation between the diseased and healthy tissues shown.

the latter agrees closely with *P. terrestris* Sherbakoff *(34)* and agrees with Dastur *(12)* that they are identical. Still more recently, Ashby *(3)* concluded, from studies of *Phytophthora* causing cacao pod rot and coconut bud rot, that they were very similar culturally and morphologically. However, as *P. faberi* Maubl. would cause coconut bud rot only when the coconut plant was

injured, and *P. palmivora* would not produce cacao pod rot, he concluded that they are two distinct organisms.

P. faberi Maubl. produces the pod rot of the cacao plant, canker in rubber trees, a rot of the papaw fruit, etc. in various tropical regions. Von Faber *(14)* noted some minor differences between this organism and *P. omnivora* as described by DeBary, but did not think the difference sufficiently great to justify establishing a new species. Nevertheless Maublanc *(13)* gave this organism specific rank, apparently from Von Faber's findings. Reinking *(26)* first decided that coconut bud rot in the Philippines was caused by an organism very similar to *Bacillus coli* but later concluded that *Phytophthora faberi* Maubl. caused the disease and that the bacteria were secondary, or, at most, only weakly parasitic. Reinking *(28)* later found, as a result of physiological and morphological studies as well as from cross inoculations, that *P. faberi* was the causal organism of coconut bud rot as well as cacao pod rot. Sharples and Lambourne *(30)*, working in Malaya, isolated from palms that had been inundated by water, three different bacteria which they used in inoculation experiments along with *P. faberi.* All plants were inoculated by puncture. All of the organisms produced bud rot symptoms in some of the plants. A high percentage of the checks also died with bud rot, yet they drew the following conclusion: "Nutritive bud-tissue of coconuts is a suitable pabulum for any saprophytic organism, either bacterium or fungus; this will develop and cause symptoms usually associated with bud rot if inoculated directly into the bud tissues." Tucker *(36)*, in Porto Rico, found that bacteria would not cause bud rot in an uninjured plant and concluded that the causal organism of coconut bud rot is *P. palmivora* and that *P. faberi* is synonymous with it.

Recent work by Leonian *(20)* tends to show that the morphology of the *Phytophthoras* is very variable and can not be depended upon with any degree of accuracy for identification of species, and that their physiology is just as variable. However, he decided that many named species could be grouped into a number of composite species. Leonian also concluded that there are numerous saltations from various species of *Phytophthora.* Gadd *(15)*, working with several strains of *P. faberi* collected from various hosts, found that these strains were very similar in morphology and physiology but fell into two groups which he considered to be biologic forms. In a more recent paper Gadd

(16a) reviews the *Phytophthoras* associated with the bud rot disease of palms and states that there are strong morphological reasons for regarding *P. faberi* and *P. palmivora* as synonyms. He concludes that it is inadvisable at present to drop either species, as the oospore stage has not been found in pure culture, although he does find that *P. palmivora* from coconut and *P. faberi* from Odontadenia yield oospores in mixed cultures.

STUDIES ON THE IDENTITY OF THE CAUSAL ORGANISM

MATERIALS AND METHODS

Until a method was devised for isolating the causal organism from bud rotted specimens, *Phytophthora* was very difficult to recover, as the specimens were frequently overrun by bacteria and fungi of various descriptions; of the latter, *Fusariums*, yeasts, *Diplodia* and *Thielaviopsis* were the most common. The first successful attempts at isolation were made by using one-fourth inch cubes of the diseased material taken from the margin of the healthy and diseased tissues. These cubes were sterilized by soaking in mercury bichloride solution, 1-1000, for five minutes, washed in sterile distilled water for a few minutes, dipped in 70 percent alcohol, flamed, and then placed in dishes of prune or corn meal agar. By using the above media the growth of bacteria was retarded somewhat. It was still farther retarded by placing the cultures in an ice box at approximately 18° C.

Later a more successful method was developed. The more badly decayed material was discarded, the outer portion of the diseased bud was removed with a scalpel, and discs, one-fourth inch in thickness, were cut from the remaining material and sterilized as described above. These sterile discs were then placed in plates containing a small quantity of distilled water. The plates were then placed in the ice box. In from 24 to 36 hours these discs were covered with a white felty growth of *Phytophthora*, in case this organism was present.

Specimens received at the laboratory were usually in varying stages of decay, but upon some of the more recently infected material there was a white felt of mycelium which often yielded pure cultures of *Phytophthora* when transferred directly to agar plates. About 25 percent of the specimens collected from 600 or more properties yielded *Phytophthora*. However, many of the collections were made from the same properties at dif-

ferent dates. These various cultures of *Phytophthora* were compared as to growth characters, spore production, and spore sizes and then classified into groups. Without exception, they readily fell into two classes or strains which were quite distinct on the basis of their reaction to various media. It seemed probable therefore that the species described in other coconut-growing regions might be nothing but strains. Accordingly, various species of *Phytophthora* which had been reported to attack palms in other countries were collected. *P. terrestris,* which is commonly found on tomato fruits in Florida, also was obtained for comparative studies.

The following cultures were compared:

8I—Isolated from bud rotted palm, collected at Miami, Fla., by G. F. Weber and identified by him as *P. faberi.*

8K—Isolated from cacao fruit, collected in the Philippines, by Otto Reinking and identified by him as *P. faberi.*

8L—Isolated from bud-rotted palm collected in Porto Rico by C. M. Tucker and identified by him as *P. palmivora.*

8M—Received from Leonian; isolated from cacao pod, collected in Jamaica by Ashby and identified by him as *P. faberi.*

8N—Received from Leonian; isolated from *Borassus flabellifer* (Palmyra palm), collected in India by Hartley and Reinking and identified as *P. palmivora.*

8P—Received from Leonian; isolated from bud rotted coconut, collected in Jamaica by Ashby and identified by him as *P. palmivora.*

8Q—Received from Leonian; isolated from tomato fruit, collected in Florida by Sherbakoff and identified by him as *P. terrestris.*

8Z—Isolated from tomato fruit, collected in Florida by G. F. Weber and identified by him as *P. terrestris.*

119—Isolated from bud rotted coconut palm, collected at Palm Beach, Florida by J. L. Seal and identified as *P. faberi.*

8X—Isolated from bud rotted coconut palm, collected at Palm Beach, Florida by Seal. This organism and many others agree with 8I and are considered to be identical with it. The remaining *Phytophthoras* isolated from bud rotted palms are considered synonymous with 119, but of these there are comparatively few in number.

The various organisms listed above were used in the laboratory and greenhouse in a general comparison as to their morphology, physiology and pathogenicity. Single spore cultures

were obtained by picking up germinating spores with the aid of a platinum needle from poured agar plates and making transfers to sterile media. Stock cultures were grown on oatmeal agar and moist, sterile corn meal. Duplicate cultures of all organisms were kept, one at room temperature (18-27°C.) and the other in the ice box (16-18°C.). The studies made in the laboratory were not entirely satisfactory, owing to the nature of the organism as well as to the lack of equipment for maintaining absolutely controlled conditions. The organisms required direct light in order to form conidia in abundance, and the temperature under such conditions fluctu-

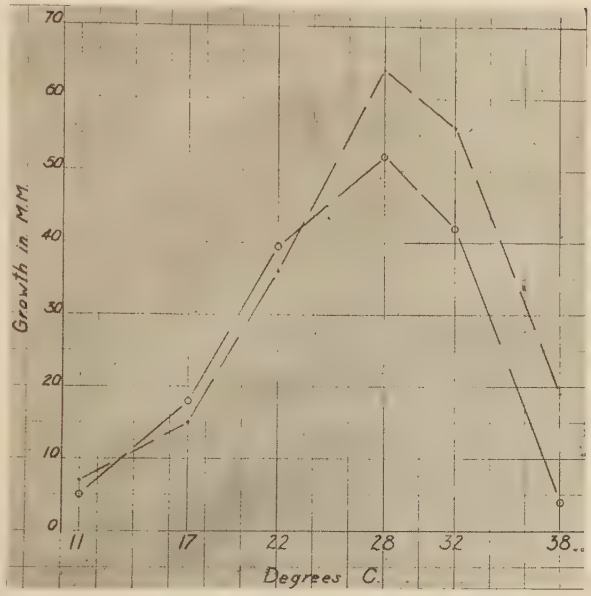

Fig. 7.—Curves showing the influence of media and tsmperature on the rate of growth of strain 8I during a period of 96 hours. Corn meal agar o——o; Prune agar ——.——.

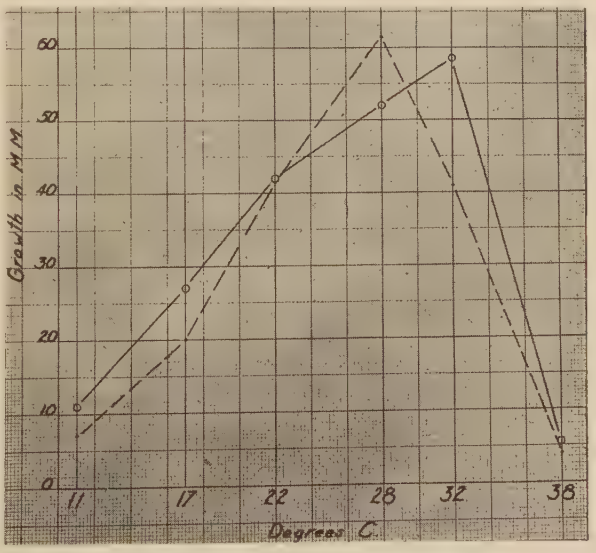

Fig. 8.—Curves showing the influence of media and temperature on the rate of growth of strain 8K during a period of 96 hours. Corn meal agar o——o. Prune agar — — —.

ated about three degrees C., but in studies where light was not a factor the temperature was controlled within two degrees.

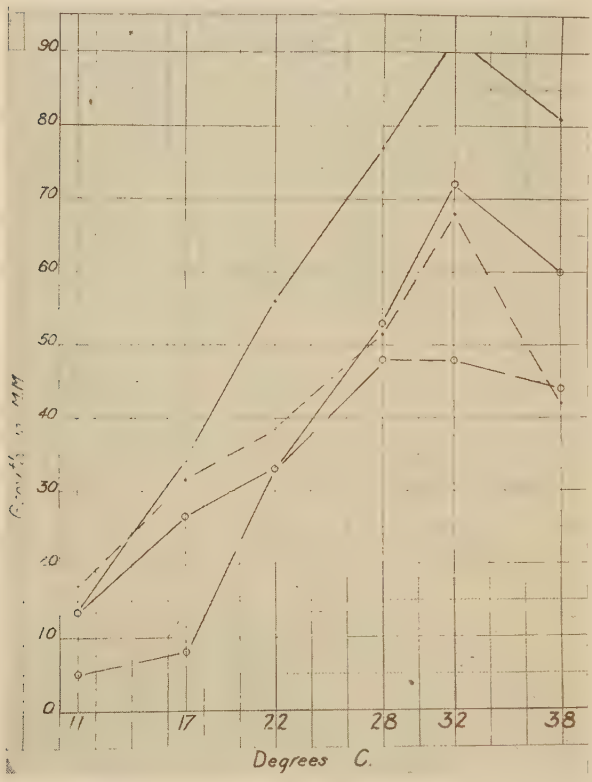

Fig. 9.—Curves showing influence of media and temperature on rate of growth of strains 8L and 119 during a period of 36 hours. 8L on corn meal agar o——o. 8L on prune agar - - - - -. 119 on corn meal agar o— —o. 119 on prune agar .— —.

Inoculations were made in the greenhouse, using potted plants that were three to six years of age. Larger plants could not be used in the greenhouse nor were inoculation experiments permitted in the field. The resistance of different aged plants to the disease has been the basis of some discussion between Sharples and Lambourne *(30)* and Sundararaman *(35)* in which the former criticised the latter for using only young plants in his inoculation experiments. Sundararaman *(35)* shows, in a more recent work, that adult trees succumb to the disease as readily as young plants. It is the primordal tissues in any case that are more readily susceptible to the organism and in these undifferentiated tissues one would find little, if any, differences, regardless of the plant's age.

PHYSIOLOGY OF THE CAUSAL ORGANISM

GROWTH ON VARIOUS MEDIA

As previously pointed out, all the different organisms react differently to different media. Furthermore, the different strains

of the same organism behave differently. When the various organisms were incubated in the light at 25°C., the exceptionally rapid growth of 119 and 8L was very noticeable, while 8Q was conspicuous because it grew slowly. The amount of aerial mycelium produced by 8N and 8Q is not so abundant as that produced by other organisms.

Just what factors cause the individual organisms to vary on a given medium has not been determined, but one of the more apparent causes seems to be moisture. On different media the various organisms react differently, as one would expect, not only in their vegetative growth but also in spore production.

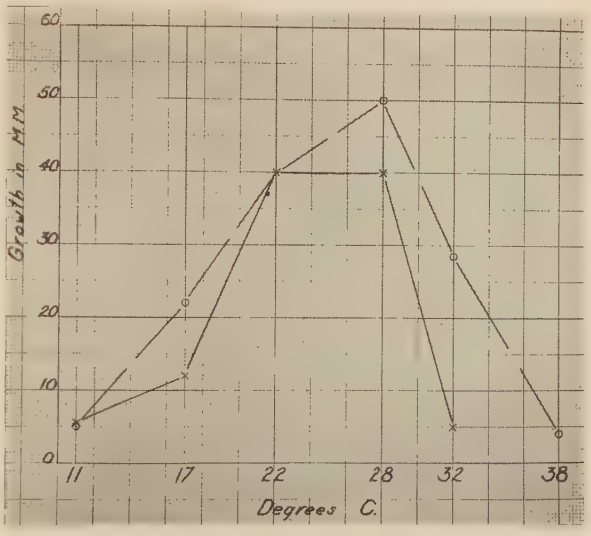

Fig. 10.—Curves showing the influence of media and temperature on the rate of growth of strain 8M during a period of 96 hours. Corn meal agar o— —o. Prune agar x——x.

The abundance of spores produced by the various organisms on the various media is indicated in Table I.

In this table one will note the scarcity of spore production in 119; also the abundance of spores produced on oatmeal agar and corn meal flour. Leonian *(20)*, Reinking *(28)*, Gadd *(15)*, Tucker *(36)*, and others have made similar observations in their studies of the *Phytophthoras*.

REACTION TO TEMPERATURE

In order to ascertain the effect of temperature on various strains and species of *Phytophthora*, parallel series of cultures on corn meal agar and on prune agar were kept at the following temperatures: 11°, 17°, 22°, 28°, 32° and 38°C. The various temperatures were obtained in a battery of soil temperature

TABLE I.—Comparative Sporulation of Different Strains and So-called Species of *Phytophthora*, on Various Media, at the End of One, Two and Four Weeks.

Organism	One Week		Two Weeks		Four Weeks	
	Conidia	Chlamydospores	Conidia	Chlamydospores	Conidia	Chlamydospores
	Potato Dextrose					
8I *P. faberi* from Florida	1	2	2	2	2	2
8K *P. faberi* from Philippines	2	2	3	3	3	3
8L *P. palmivora* from Porto Rico	0	0	1	0	1	1
8M *P. palmivora* from Jamaica	2	2	3	3	3	3
8N *P. palmivora* from India	0	0	1	0	1	1
8P *P. palmivora* from Jamaica	2	0	4	1	4	2
8Q *P. terrestris* from Florida	2	0	3	2	3	3
119 *P. faberi* from Florida	0	0	1	1	1	1
	Oat Meal Agar					
8I *P. faberi* from Florida	1	2	3	3	3	3
8K *P. faberi* from Philippines	2	3	3	4	3	4
8L *P. palmivora* from Porto Rico	1	1	2	2	2	2
8M *P. palmivora* from Jamaica	3	1	4	3	4	3
8N *P. palmivora* from India	1	0	2	0	2	0
8P *P. palmivora* from Jamaica	3	3	4	4	4	4
8Q *P. terrestris* from Florida	2	2	3	3	3	4
119 *P. faberi* from Florida	0	0	1	1	1	1
	Corn Meal Flour					
8I *P. faberi* from Florida	2	2	3	2	3	3
8K *P. faberi* from Philippines	3	3	4	3	4	4
8L *P. palmivora* from Porto Rico	2	3	3	4	3	4
8M *P. palmivora* from Jamaica	3	3	4	4	3	4
8N *P. palmivora* from India	1	0	2	0	2	0
8P *P. palmivora* from Jamaica	3	3	4	4	4	4
8Q *P. terrestris* from Florida	2	2	3	3	3	4
119 *P. faberi* from Florida	0	0	0	1	0	1
	Corn Meal Agar					
8I *P. faberi* from Florida	2	2	3	3	2	3
8K *P. faberi* from Philippines	2	2	3	2	2	3
8L *P. palmivora* from Porto Rico	2	0	2	1	2	2
8M *P. palmivora* from Jamaica	2	2	3	3	2	3
8N *P. palmivora* from India	1	0	2	0	2	1
8P *P. palmivora* from Jamaica	2	1	3	2	2	3
8Q *P. terrestris* from Florida	1	0	2	1	2	2
119 *P. faberi* from Florida	0	0	1	1	1	1

0—None.
1—Very scarce.
2—Scarce.
3—Abundant.
4—Very abundant.

tanks in which soil cans were suspended in water. The temperatures were regulated by thermostat-controlled kelvinator and electrical heating units. The temperature did not vary more than two degrees C. in each series. The media were prepared from

dehydrated agars[5] in which the pH tested 6.8. Plates were poured and held at room temperature for 24 hours, after which they were inoculated. The inoculated plates were held at 25°C. for 12 hours, at which time the contaminated plates were discarded and the uncontaminated ones placed at the various temperatures. Five plates of each organism were incubated at each temperature and measurements of each organism were made at intervals of 12 hours up to the 96th hour. This experiment was repeated, and, from the averages of the various diameters of each organism, curves were plotted as shown in figures 7 to 15. In these figures the rate of growth of the various organisms is compared on corn meal agar and prune agar. Very slight growth was noted for all the organisms at 11°C., with the exception of 8P, which made a perceptible growth on corn meal agar. (Fig. 12.) The rate of growth gradually increases with increased temperature up to 28°C. and, in some cases, up to 32°C.

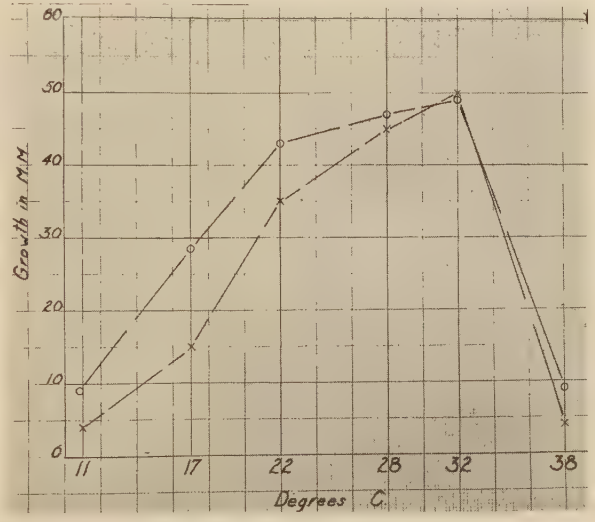

Fig. 11.—Curves showing the influence of media and temperature on the rate of growth of strain 8N during a period of 96 hours. Corn meal agar o— —o. Prune agar x— —x.

In 8I, 8M, 8P and 8Q, the optimum vegetative growth is reached at 28°C; while in 8K the optimum lies between 28° and 32°C; and in 8L, 8N and 119 the optimum is 32°C. The maximum differs for the various organisms, extending from 32° to

[5]Manufactured by the Digestive Ferments Co.
Prune agar—20 grams dehydrated agar was added to 1000 cc. water and autoclaved.
Corn meal agar—19 grams dehydrated agar was added to 1000 cc. water and autoclaved.
Potato Dextrose—20 grams dehydrated agar was added to 1000 cc. water and autoclaved.

38°C, the maximum depending upon the substratum on which the organism is grown. On corn meal agar 8L and 119 grow exceptionally well at 38°, while the other organisms grow very poorly at this temperature (see Fig. 9). On prune agar the various organisms act, in general, very much like they do on corn meal agar, with the outstanding exception of 8M, which has its optimum between 22° and 28° instead of between 28° and 32°C. The organism grew more vigorously on prune agar than on corn meal agar, while the latter was conducive to a more uniform growth of the various organisms. Reinking *(28)* reported the optimum temperature for growth of 8K as lying between 27° and 30°C., being nearer 27°. This discrepancy may be due to the substratum, as Reinking's results were obtained on potato dextrose agar.

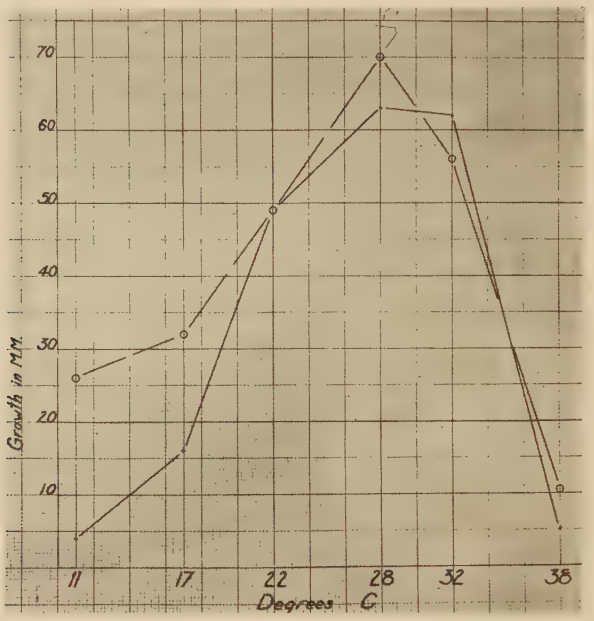

Fig. 12.—Curves showing the influence of media and temperature on the rate of growth of strain 8P during a period of 96 hours. Corn meal agar o— —o. Prune agar .——.

REACTION TO LIGHT

Light was excluded from the temperature chambers and consequently very few conidia were produced in any of the cultures. When they did occur, they were found in cultures incubated at 22° to 32°, with an occasional one in cultures incubated at 17° and at 32°C. Chlamydospores were not formed because of the limited period of the experiments. The mycelium was usually appressed or submerged at 11° and 17° and in all cases the same condition prevailed at 38°, with the exception of 119 and 8L, where a fluffy growth was evident. All of the organisms produced an abundance of aerial mycelium between 22°

and 32° except in the case of 8M, in which the aerial mycelium was very light under the best of conditions.

MORPHOLOGY OF THE CAUSAL ORGANISM

MYCELIUM

There is not much difference in the mycelium of the various strains, although there are some differences in quantity, size and uniformity on various media. The aerial hyphae are colorless, straight, more or less uniform in size, branching freely, slightly constricted where branches arise from the older hyphae. The contents of young hyphae are granular but become vacuolated with age, and oil globules are common. Submerged mycelium may be straight or irregular, smooth to uneven,

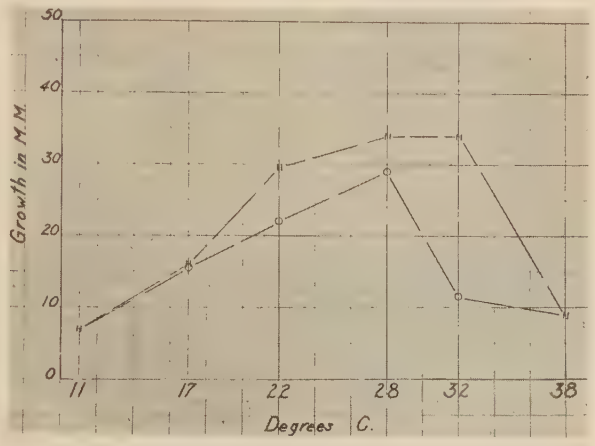

Fig. 13.—Curves showing the influence of media and temperature on the rate of growth of strain 8Q during a period of 96 hours. Corn meal agar o— —o. Prune agar 11— —11.

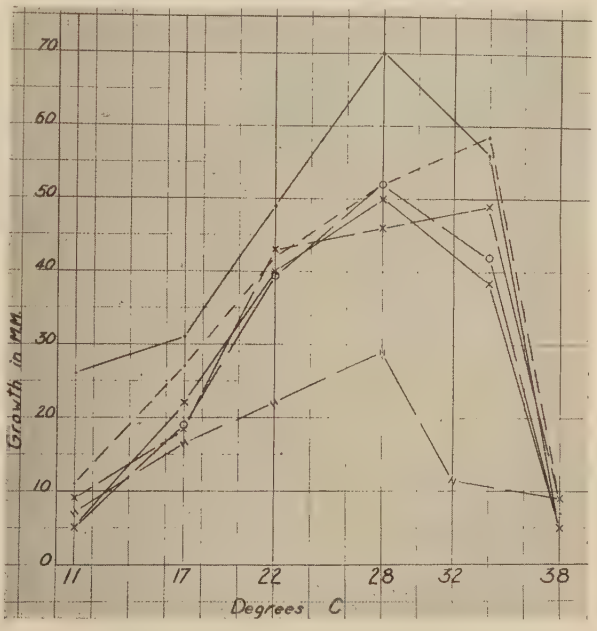

Fig. 14.—Curves showing the influence of temperature on the rate of growth of the various strains when grown on corn meal agar for a period of 96 hours. 8I o——o. 8K .— —. 8L x— —x. 8M x——x. 8P .——. 8Q 11——11.

gnarled or even warty, branching freely but irregularly, turning from hyaline to yellow and varying in diameter from 3μ to 11μ. The mycelium usually is non-septate when young but later a few septa are formed in the vegetative as well as in the fructifying hyphae. Mycelium is abundant in the host, intercellular and sends fingerlike haustoria into the cells. (See Fig. 16.)

In plate cultures the first mycelial growth is submerged, but after 24 to 48 hours aerial mycelium becomes visible. At first it is very scant but soon becomes more dense. In most of these organisms the submerged mycelium is as described above except that of 8Q, which may be warty. The aerial mycelium remains fluffy for a week or 10 days, after which it becomes prone and lightly to heavily massed on the surface of the substratum. Conidia sometimes are formed on the aerial mycelium within four days, but it is usually about the seventh day before large numbers of the spores are formed.

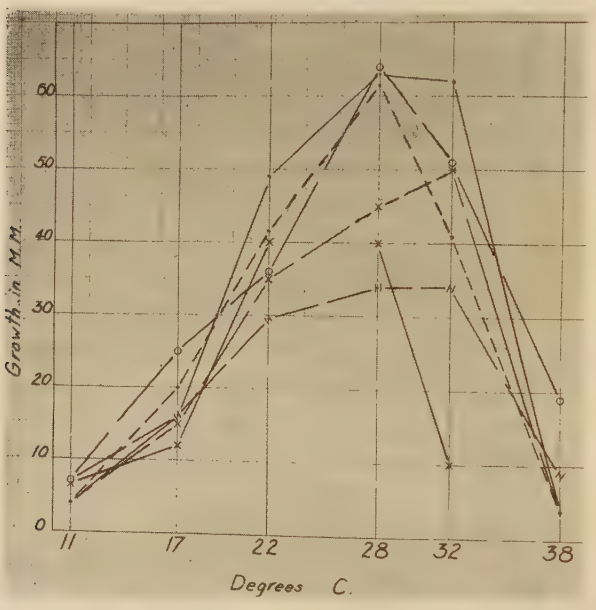

Fig. 15.—Curves showing the effect of temperature on the rate of growth of the various strains when grown on prune agar for a period of 96 hours. 8I o——o. 8K .— —. 8L x— —x. 8M x——x. 8P .——. 8Q 11— —11.

CONIDIOPHORES

The width of the conidiophores is less than that of the average mycelium, being only 3μ to 8μ, and more commonly about 5μ. The conidiophores may be short or long, ranging from 150 to 750μ.

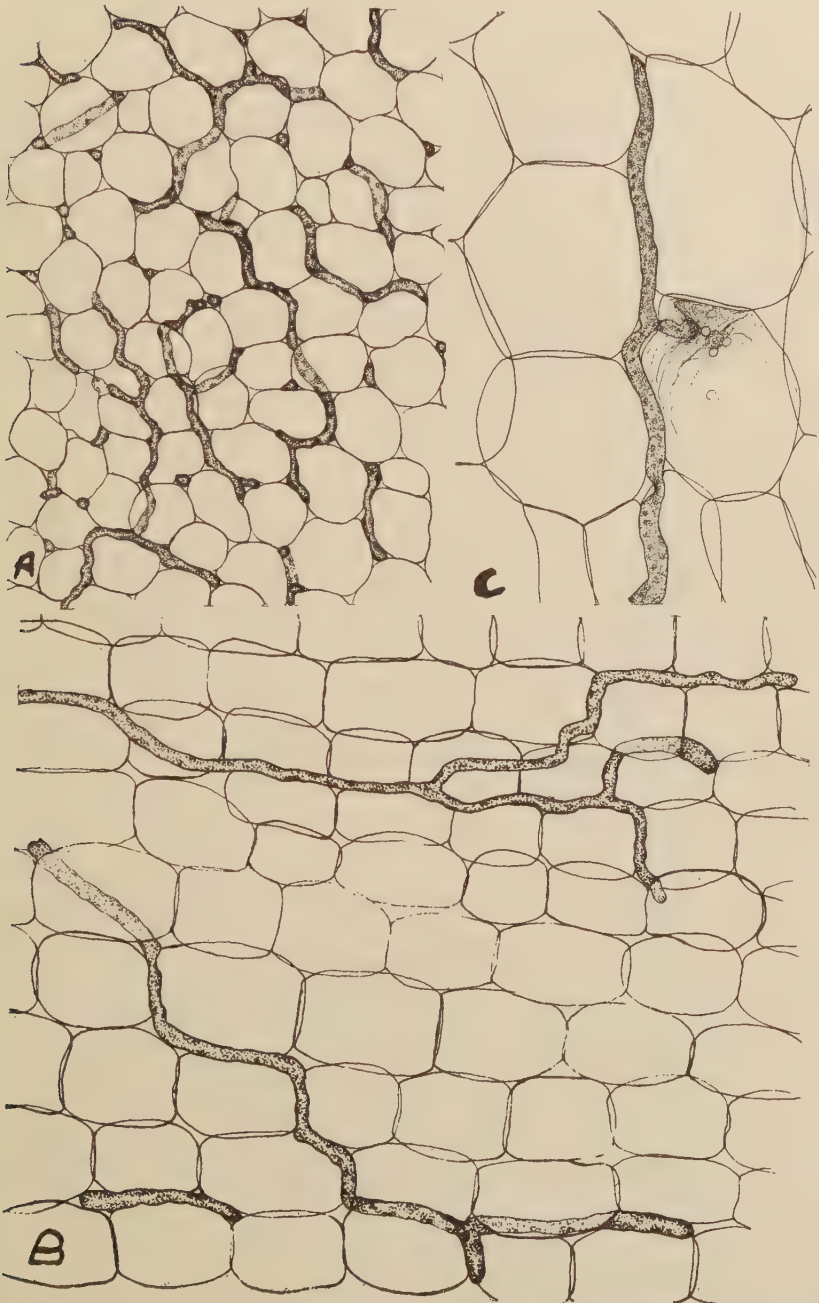

Fig. 16.—Camera lucida drawings of section of bud rot tissues. A—Cross section showing the intercellular mycelia. B—Tangential sections showing a strand of intercellular mycelium. C—Tangential section showing a strand of intercellular mycelium sending haustoria into one of the host cells. (A and B x 250. C x 500.)

The number of spores produced on a single conidiophore varies from one to 20, but usually there are from five to 10. Gadd *(15)* reports that the conidiophores of different strains bear different numbers of spores. Usually there are from one to eight branches and each branch bears only one spore, as shown in Fig. 19. The type of sporophore branching varies considerably in the various strains, as shown in figures 18 and 19. In most strains the sporophore is very compact, as the spores are borne on short pedicels. In other strains the spores are borne on exceedingly long pedicels and the sporophore is of a spreading type. Reinking *(28)* does not note this latter type of sporophore, but it is very clearly shown by Rosenbaum *(29)*. Spores are borne terminally and the mycelium continues its growth as the spore is cut off with a short stalk or pedicel. The best method found for studying the conidiophores is to stain the organism while in a fructifying state in a petri dish. In order to do this, the organism was killed by flooding it with 95 percent alcohol which was drained off after a few minutes; and the culture was then stained with 1 percent acid fuchin, washed with 50 percent alcohol and then with water. In such preparations the conidiophores can be studied under the low power of the microscope, while still on the medium or after having been transferred to a slide.

CONIDIA

Conidia are produced terminally on the sporophores and, in artificial cultures, may be abundant or completely absent. They are oval to oblong with a papilla which is very prominent on the more spherical ones and only slightly evident on the oblong ones. (Figures 20 and 21.) The spores are generally attached at the blunt end to the sporophore but occasionally this attachment is at the side of the spore, as in Fig. 20.

Spores are shed from the sporophore with or without a pedicel, which varies from 3 to 6μ in length. (See Fig. 20.) The spores are hyaline or only slightly yellow when young, multinucleate, and finely granular, but they may become a distinct yellow on ageing, and may become vacuolate and coarsely granular with many oil globules. The walls are thin and colorless at first, but thicken and darken upon becoming old.

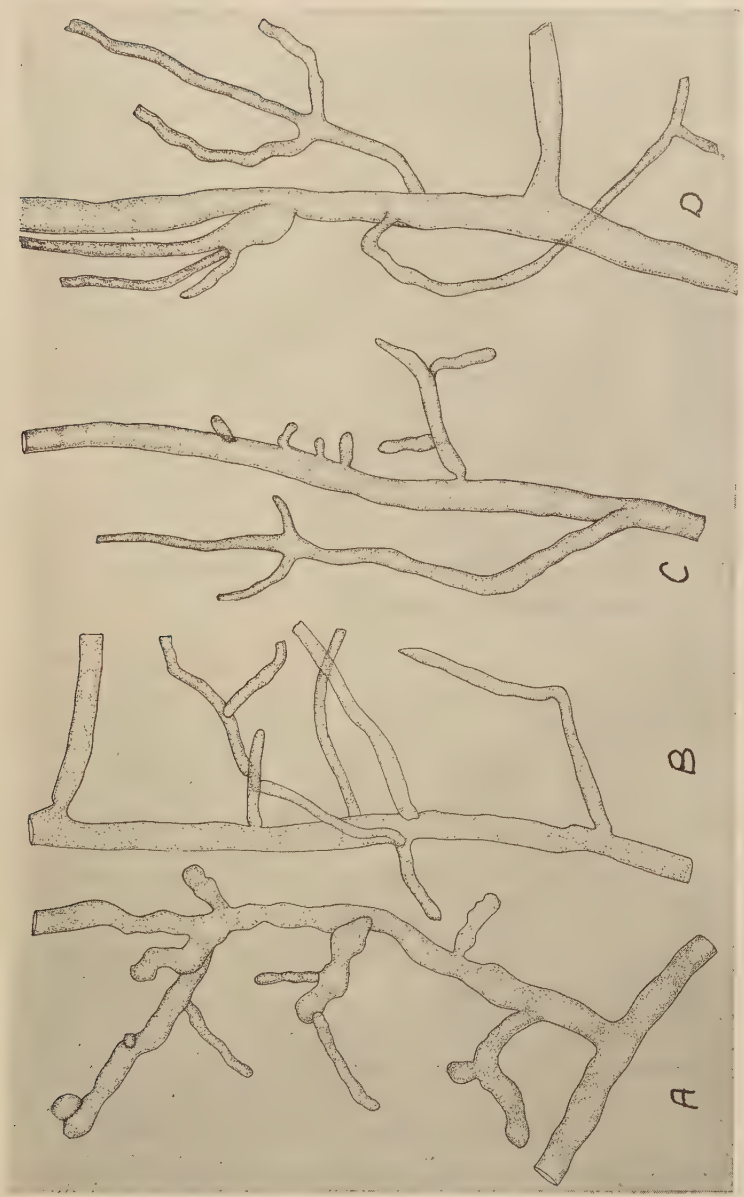

Fig. 17.—Vegetative hyphae of different strains which give rise to the sporophores. A—*Phytophthora terrestris*. B—*P. faberi*. C and D—*P. palmivora*. (All x 750.)

CHLAMYDOSPORES

Chlamydospores are generally produced under all conditions to which the various fungi have been subjected and are the most common spore form under all conditions. They frequently occur in diseased tissue and on artificial media, but their abundance depends to a considerable degree upon the substratum upon which the organism is grown. Light does not play the important role in their development that it does in the development of conidia. The chlamydospores are produced primarily in an intercellular manner, but they may be produced terminally on short branches which are perpendicular to the vegetative hyphae. The shape may be irregular or perfectly spherical. Usually it varies first in the diameter of one axis and then in the other and, upon averaging the dimensions a large number of the spores, insignificant difference is noted between measurements in diameter of the two axes. While young they are slightly yellow to hyaline, granular, slightly vacuolate, with a hyaline, thin wall, but as the spore ages the color becomes yellow, and, in some instances, turns to a light shade of brown, granulation becomes less uniform, vacuoles enlarge, and spore walls thicken to even twice the original thickness.

OOSPORES

Oospores have not been found in any of the many artificial cultures examined nor in any of the bud rotted specimens. If they are formed in artificial media or in diseased plants, they must be exceedingly rare. Rosenbaum *(29)*, Reinking *(28)*, Tucker *(30)*, and Butler *(7)* failed to find this spore form in the host or the culture media. Ashby *(2)* reports finding a few in host tissue, while Gadd *(15)* was unable to find them in host tissues or in artificial cultures of an individual strain. However, when he placed two strains in the same culture, oospores were produced. He therefore concluded that the organisms are heterothallic. No attempt has been made in the present work to see if the various strains would yield oospores under the above conditions.

SPORE MEASUREMENTS

Spore dimensions have been successfully used as a means of delimiting species. This character, however, has proved to be quite variable, the variability sometimes being due to a number of different factors, including biologic forms with a Linnean

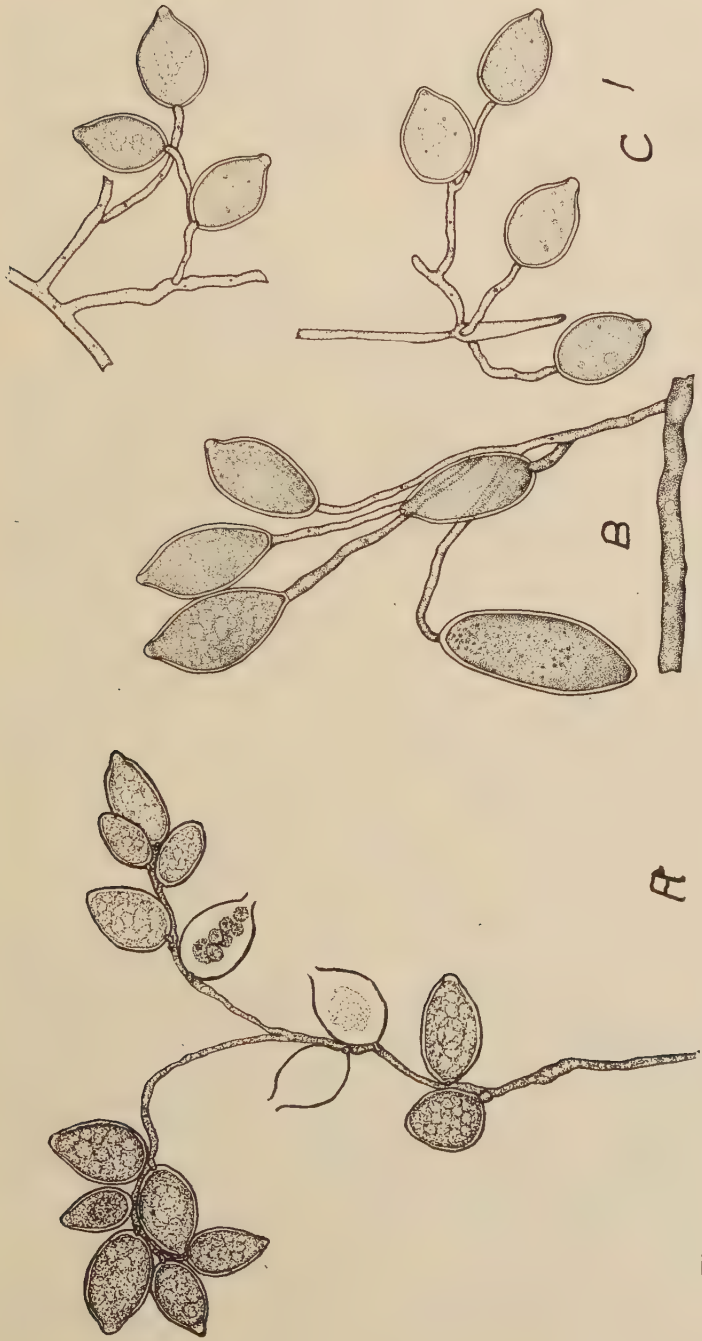

Fig. 18.—Conidiophores and conidia of different *Phytophthora* (x 375). A—*P. faberi* from the Philippines. B—*P. palmivora* from Jamaica. C—*P. palmivora* from India.

species. Stakman and Levine *(33)* and Levine *(22)* have shown that the biologic forms of *Puccinia graminis* Erikss. and Henn. can be distinguished on the basis of spore size if sufficient spores are measured, provided they were produced under normal and uniform conditions. LaRue and Bartlett *(18)* have also dis-

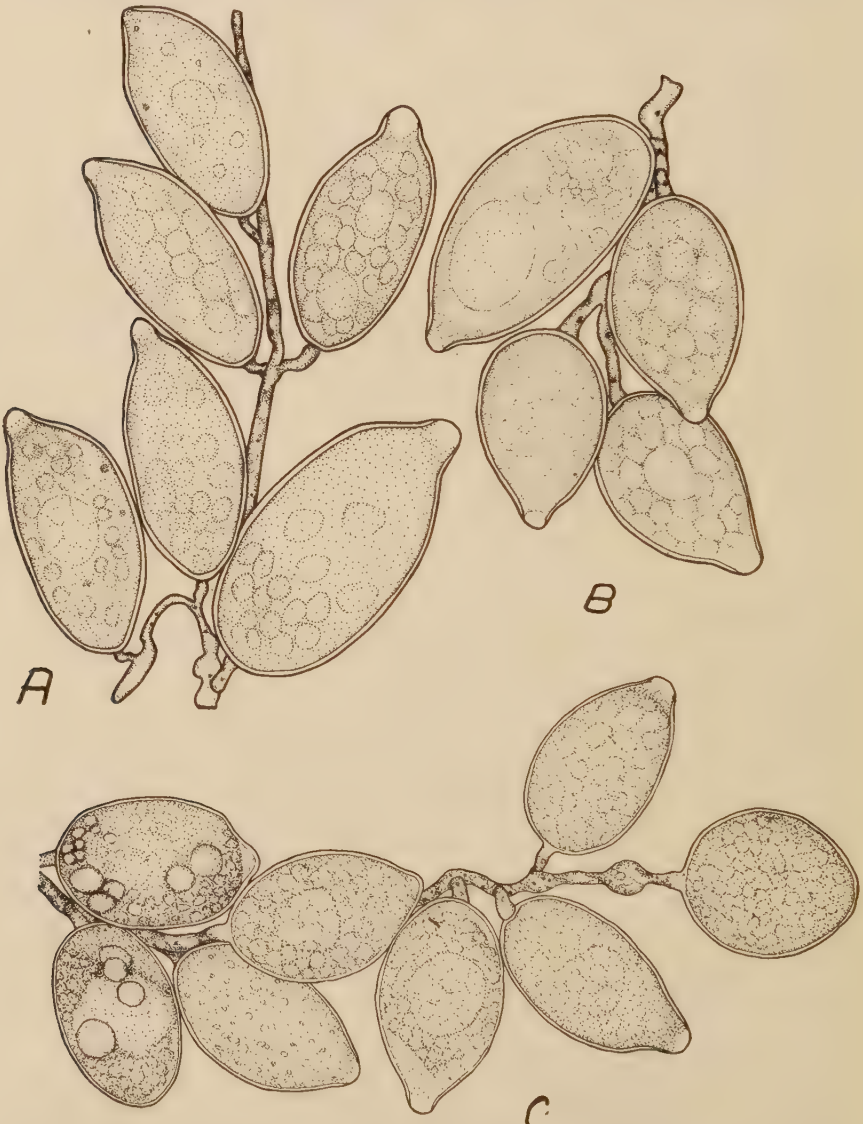

Fig. 19.—Conidiophores and conidia of different Phytophthoras (x 750). A—*P. faberi* from Florida. B—*P. palmivora* from Porto Rico. C—*P. faberi* from Jamaica.

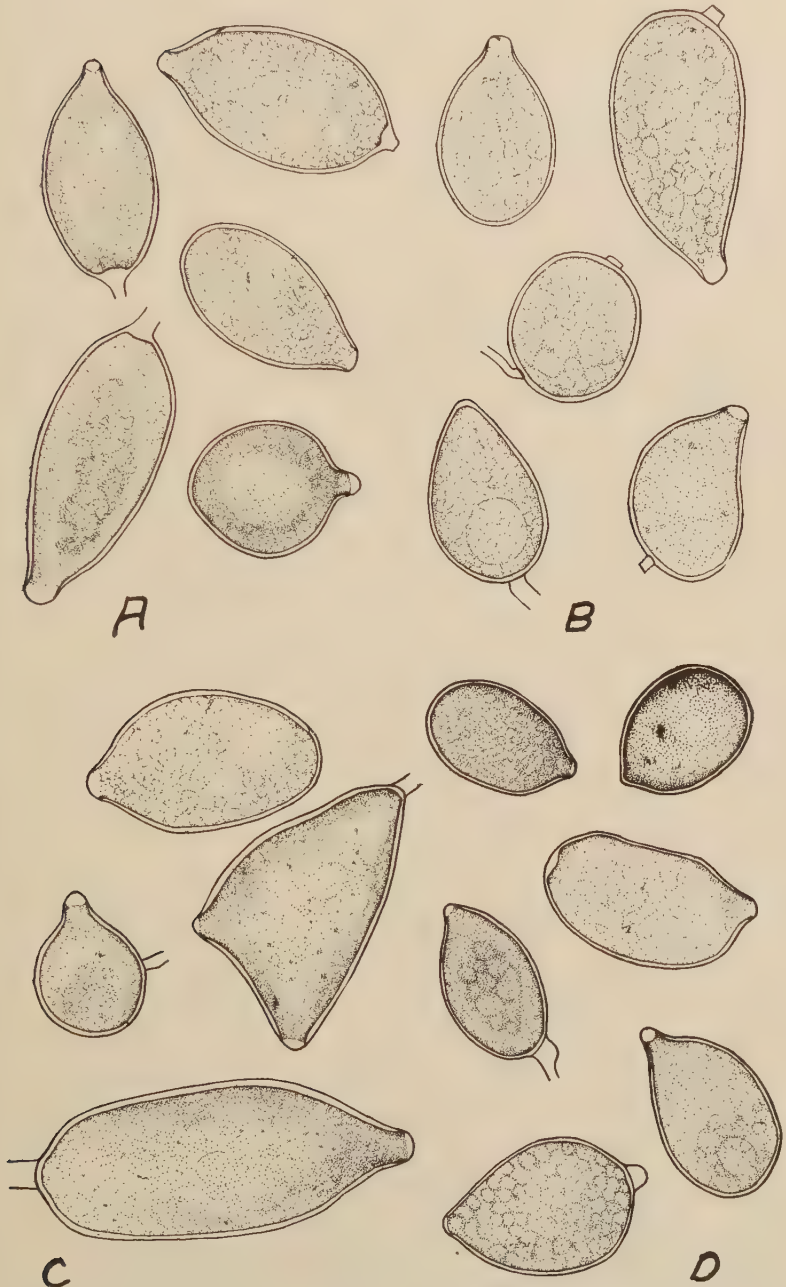

Fig. 20.—Types of conidia produced by the different Phytophthoras (x 750). A—*P. faberi* from Florida. B—*P. palmivora* from Jamaica. C—*P. faberi* from India. D—*P. faberi* from Jamaica.

tinguished numerous strains of *Pestalozzia guepini* Desm. on the basis of spore size. Burger *(5)* found a great difference in size of spores of several strains of *Colletotrichum gloesporioides* Penz., in which he observed that the medium had a marked effect on spore size, but did not necessarily affect each strain in the same manner.

Leach *(19)*, working with various biologic forms of *Colletotrichum lindemuthianum* (Sac. and Mag.) Bri. and Cav., concludes that differences influenced by the culture media on spore size were so great and that the difference between the various strains in regard to spore size was so small that the results obtained from spore measurements were of no practical value. Gadd *(15)*, working with six strains of *Phytophthora faberi* Maubl., gives evidence that there are real differences in spore sizes of these strains and that the conditions under which the organism is grown, i. e. media, light, temperature, moisture, aeration, etc., have some influence upon the spore size. Ashby *(2)* states that age influences the size of spores. The first spores produced by the organism are larger than those produced later.

There is considerable difference in the spore dimensions of the different *Phytophthoras* attacking the coconut palm, as given by the various workers. These discrepancies may be accounted for on the basis of variance of biologic forms, habitat, climatic conditions, age, number of spores measured, experimental error, etc.

In an effort to determine the limits of variation in spore size of the *Phytophthoras* attacking the coconut palm, the organisms were grown on four of the more common artificial media: potato dextrose agar, oatmeal agar, corn meal agar, and sterilized corn meal flour. The measurements were made of spores obtained from cultures of the various strains of *Phytophthora* which were grown on the same batch of media, incubated at the same temperature, and measured at as near the same age of development as possible. Conidial measurements were always made as soon as enough spores had been formed in the culture, in order to eliminate secondary conidia. The same microscope and micrometer were used in making all the measurements.

Measurements were made at the interpupillary distance of 60 mm., with a 4 mm. objective, a 10X ocular and with the aid of an eyepiece micrometer in which each division was equivalent

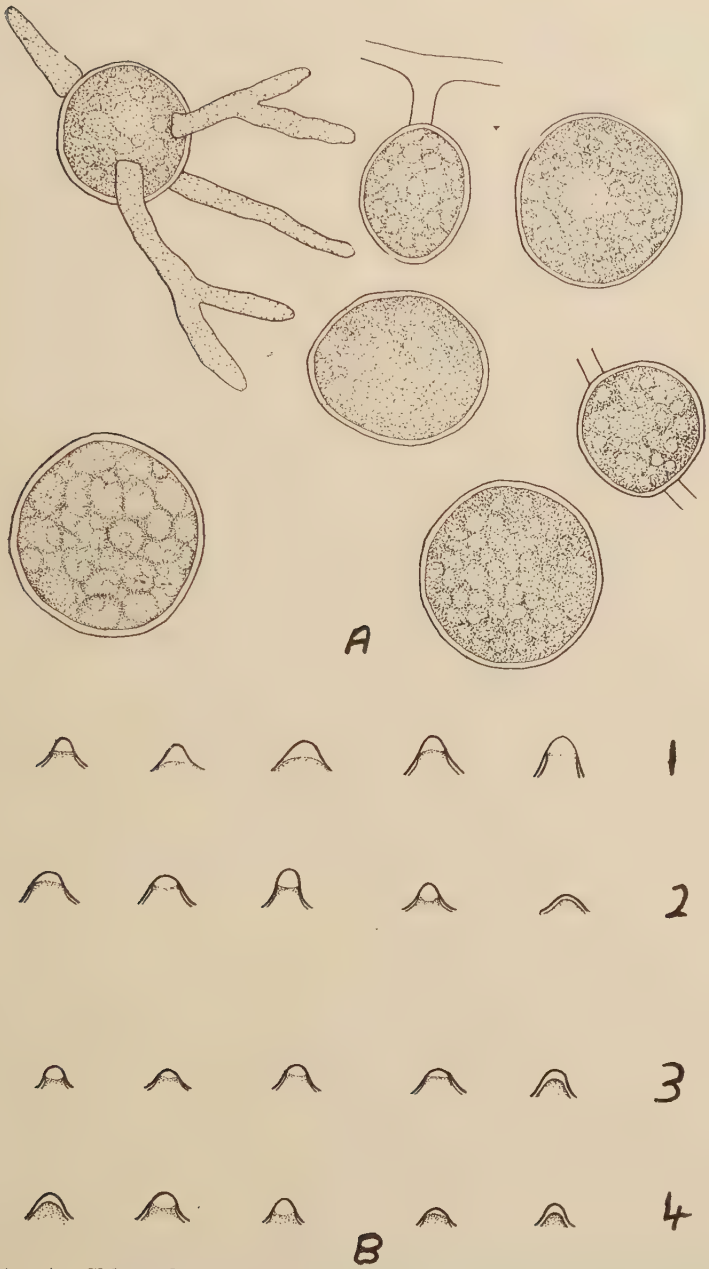

Fig. 21.—A, Chlamydospores, showing method of production, shape and germination (x 500). B, Terminal papillae from conidia of different Phytophthoras. 1. *P. faberi* from Florida. 2. *P. faberi* from the Philippines. 3. *P. faberi* from Jamaica. 4. *P. terrestris* from Florida. (x 500).

to 1.57μ. Four or more mountings of the organism measured were used and these were taken from different places of the culture which were grown in test tubes. In order that the samples of a given organism might be representative, 400 spores of each spore type were measured; this number seemed to be sufficient in most cases. As the ratio of conidial width to length was to be determined, length and width of each spore measured was noted. For length, the conidia were measured from the tip of the papillum to the base, exclusive of the basal stalk; the width was obtained by measuring the largest diameter of the breadth of the conidia.

In the biometric studies calculations were made according to the methods given by Babcock and Clausen *(4)*. In order to interpret the differences found in such a study it was necessary to calculate the probable error of these differences and then establish relationship between the differences and their probable errors. Rietz and Smith *(25)* make the following statement with reference to the significance of the probable errors: "If the difference does not exceed two or three times the probable error, the difference may be reasonably attributed to random sampling. If the difference between the two results is as much as five to ten times the probable error the probability of such differences in random selection is so small that we are justified in saying that the difference is significant." In the present study a difference less than five times the probable error of this difference was considered questionable, and only differences as great as or greater than five times the probable error were considered as really significant.

In Table II is a summary of the spore measurements of all the strains studied, when grown on the four different media under conditions that were similar in all respects. In this table the classes are arranged according to length and width of conidia, each class differing from the other by 1.57 microns. This table also shows the number of spores falling into each class. The chlamydospore dimensions are summarized in a similar way in Table III.

Tables IV, V and VI are so arranged as to show the range of variations in the spore dimensions and to give the constants with their probable errors for the different spore types of the different strains of *Phytophthora* grown on the same and on different substrata.

TABLE II.—Frequency Distribution According to Size of Conidia of Cer

Classes According to Length and Width in Microns	Potato Dextrose Agar												Oat M					
	8I		8K		8L		8M		8P		8Q		8I		8K		8 L	
	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
14.13																		
15.70												1						
17.27				1								1						
18.84		2		1								2		1				
20.41		5		5		4		2				6		5				2
21.98	1	12		14		11		8				25		19				9
23.55	2	28		33		34		16		10		51		45		2	1	29
25.12	4	53	1	38		97		39		22	2	68		66		3	0	58
26.69	5	73	2	61		111		56		43	3	68		73		6	1	79
28.26	7	75	2	72	3	89	2	81		79	5	59	6	55	1	18	1	74
29.83	8	61	5	71	6	36	2	62	1	85	13	46	6	41	0	25	3	59
31.40	13	46	15	53	10	9	11	63	3	65	23	26	14	33	1	44	4	40
32.97	15	24	27	26	18	6	16	34	2	45	32	17	13	25	0	69	12	26
34.54	25	12	30	13	37	2	25	18	7	24	40	15	17	18	2	58	19	11
36.11	30	5	29	6	51	1	29	10	12	15	51	7	29	11	1	58	33	6
37.68	40	3	44	5	64		36	7	18	8	49	5	30	6	3	50	40	4
39.25	45	1	38	1	62		50	3	26	3	42	2	33	2	5	34	42	1
40.82	50		48		42		50	1	44	1	40	1	32	0	5	20	46	2
42.39	40		42		38		40		41		28		29		4	8	42	
43.96	36		31		27		37		40		17		29		12	3	38	
45.53	24		24		19		32		39		10		19		18	2	25	
47.10	15		14		10		29		33		17		23		25		22	
48.67	12		15		7		10		37		8		19		27		11	
50.24	9		14		3		15		33		7		23		30		14	
51.81	7		9		3		7		20		7		11		32		9	
53.38	5		3				4		18		4		15		34		10	
54.95	4		1				2		8		1		12		35		6	
56.52	2		2				2		7		1		14		29		11	
58.09	1		2				1		4				8		25		2	
59.66			1						1				7		28		2	
61.23			0						2				2		24		1	
62.80			1						1				5		15		1	
64.37									2				1		12		1	
65.94									1				1		9		1	
67.51													7		7		2	
69.08													1		6			
70.65													0		2			
72.22															4			
73.79															0			
75.36															1			
76.93															1			
78.50															1			
80.07															0			
81.64															1			
83.21																		
84.78																		
86.35																		
87.92																		
89.49																		
91.06																		
92.63																		
94.20																		
95.77																		

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. Palmivora* fr
8M—*P. faberi* from

a Grown on Various Media but Under Uniform Environmental Conditions; uals.

Corn Meal Flour										Corn Meal Agar											
8L		8M		8N		8P		8Q		8I		8K		8L		8M		8N		8P	
Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
			1												1						
			0								3		0								
			2								6		1				1		1		3
			5		2						19		6				1		2		13
		1	13		14		2		3		60		30		3		7		7		33
		2	28		39		5		7	1	73		61		4		27		15		68
2		3	41		74		28		13	2	73		81	1	10		52		28	1	80
12	3	5	45		79		54		17	4	59		61	1	19		94	3	61	2	68
14	3	5	57	1	76		77		41	12	59	6	58	3	47	4	82	5	67	8	66
33	15	14	68	1	57	1	99	1	43	22	27	22	46	3	61	5	56	8	76	11	41
59	37	14	50	4	33	0	54	3	44	19	14	19	27	2	71	8	24	6	61	11	15
68	82	20	33	7	13	2	35	3	54	29	3	25	26	4	60	8	32	6	45	12	8
74	95	20	27	3	5	1	23	8	58	41	4	47	6	6	43	20	14	24	16	23	5
64	64	23	18	11	6	8	9	7	48	46		54	4	11	33	44	7	26	14	33	
38	3 50	34	8	29	1	16	6	5	32	56		39	1	14	23	61	0	47	6	37	
23	3 30	29	2	21		28	6	16	14	34		43	1	23	13	59	2	40	1	54	
7	8 13	29	2	33	1	35	1	25	17	35		37		29	7	47	1	51		44	
4	11 4	39		34	0	41	0	19	7	29		29		48	4	51		61		43	
2	16 4	33		40		32	1	26	1	26		25		46	1	34		29		37	
	41	32		42		40		36		14		18		40	1	24		25		26	
	35	28		34		28		37	1	11		6		40		12		21		15	
	37	17		27		38		31		6		7		31		18		15		12	
	49	17		30		26		29		4		5		27		11		10		12	
	45	14		27		24		28		4		3		20		5		7		9	
	41	7		16		17		25		2		3		18		2		5		4	
	22	4		11		19		19		1		1		10		2		4		3	
	21	7		7		14		26		2		0		9		1		2		2	
	21	2		6		12		22				1		7		3		1		1	
	18	1		4		9		15						5		0		1			
	14			6		6		8						1		1		2			
	4			2		3		5						1				1			
	3			1		2		2													
	3			1		1		1													
	2			1		0		2													
	1			1		1		1													
	1																				
	0																				
	0																				
	1																				

palmivora from India
palmivora from Jamaica

8Q—*P. terrestris* from Florida

The probable error of the differences in the statistical results obtained in this study are given in Tables VII and VIII. The various strains are grouped according to the substrata on which they were produced.

In figures 22 to 36 curves are plotted for spore dimensions in microns. These graphs represent the variation in spore sizes of the various strains when the organisms were grown on various media and on the same media, but in either case under uniform environmental conditions.

TABLE III.—Frequency Distribution, According to Size of Chlamydospores of Certain Strains and Species of *Phytophthora* Grown on Various Media but Under Uniform Environmental Conditions; Population in Each Case = 400 Individuals.

Classes According to Diameter in Microns	Media																	
	Potato Dextrose Agar						Oat Meal Agar						Corn Meal Agar					
	8I	8K	8L	8M	8P	8Q	8I	8K	8L	8M	8P	8Q	8I	8K	8L	8M	8P	8Q
15.70				1	1	1	1				1							
17.27				3	1	2	1				0							
18.24			1	7	1	5	3	2			1		1			2	1	
20.41	3	2	3	11	4	8	5	2	1		2	1	3			2	1	
21.98	8	4	3	19	4	14	6	3	1	1	3	2	3	1	1	5	1	1
23.55	14	9	6	28	11	29	12	4	2	3	5	4	5	2	3	8	4	2
25.12	24	5	12	39	26	47	25	7	8	5	17	6	9	4	4	22	8	4
26.69	38	10	19	35	41	54	32	10	19	4	27	15	12	7	20	22	11	12
28.26	42	23	21	41	52	56	39	15	23	5	38	21	21	9	25	32	14	14
29.83	38	28	24	52	54	50	45	13	34	10	38	24	20	6	33	39	19	22
31.40	41	28	37	48	57	37	43	18	57	17	42	34	40	10	51	34	31	28
32.97	45	29	41	33	52	31	50	24	56	30	51	40	54	11	67	48	44	34
34.54	53	32	51	26	31	16	36	35	57	37	47	42	57	16	79	34	57	49
36.11	27	33	45	28	27	17	31	38	59	43	49	41	51	27	53	40	53	50
37.68	25	42	44	13	17	11	23	42	37	49	36	39	45	29	29	26	55	46
39.25	14	37	31	8	12	8	20	43	21	55	23	37	37	36	20	31	38	33
40.82	16	34	21	3	4	7	16	39	14	56	8	34	21	57	7	21	28	27
42.39	7	23	20	2	2	4	7	29	6	31	7	18	11	43	3	19	19	24
43.96	3	25	8	2	1	2	3	21	3	29	3	13	7	47	2	10	9	19
45.53	1	18	6	1	1	1	1	22	1	10	1	10	2	26	2	3	5	13
47.10	1	9	3		1		1	9	1	6	1	6	1	17	1	1	1	11
48.67		4	2					7		4		4		13		1	1	6
50.24		2	1					5		3		4		16				3
51.81		0	1					4		1		2		6				1
53.38		2						2				2		7				1
54.95		0						2				1		3				
56.52		1						2						5				
58.09								1						2				
59.66								1										

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

TABLE IV.—Variations and Constants for Lengths of 400 Conidia of Strains of *Phytophthoras* Grown on Various Media Under Uniform Environmental Conditions.

Strains	Media*	Spore Classes According to Length in Microns																									Mean	Deviation Standard	Coefficient of Variability
		19.63	22.77	25.91	29.05	32.19	35.33	38.47	41.61	44.75	47.89	51.03	54.17	57.31	60.45	63.59	66.73	69.87	73.01	76.15	79.29	82.43	85.57	88.71	91.85	94.99			
8I	P.A.	.....	3	9	15	28	55	85	90	60	27	16	9	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.13± .21	6.20± .15	18.39± .44
	O.A.	.....	.....	.....	12	27	46	63	61	48	42	34	27	22	9	6	2	1	.....	.....	.....	.....	.....	.....	.....	.....	43.38± .30	8.78± .20	19.43± .47
	C.A.	.....	3	16	41	70	102	69	55	25	10	6	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	36.38± .20	5.83± .14	13.45± .32
	C.F.	.....	.....	9	14	14	39	54	78	70	46	37	17	12	7	2	0	1	.....	.....	.....	.....	.....	.....	.....	.....	43.11± .17	7.33± .17	17.01± .40
8K	P.A.	.....	.....	3	7	42	59	82	90	55	29	23	4	4	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	40.58± .21	6.09± .14	15.01± .36
	O.A.	.....	.....	.....	1	1	3	8	9	30	52	62	69	54	52	27	16	8	4	2	1	1	.....	.....	.....	.....	54.43± .26	7.63± .16	14.02± .33
	C.A.	.....	.....	6	41	82	93	80	54	24	12	6	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	36.66± .18	5.30± .13	14.45± .34
	C.F.	.....	.....	.....	3	4	7	20	33	46	53	83	62	37	25	9	8	5	4	1	.....	.....	.....	.....	.....	.....	50.55± .27	7.90± .18	15.63± .37
8L	P.A.	.....	.....	.....	9	28	88	126	80	46	17	6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.00± .15	4.33± .10	11.13± .26
	O.A.	.....	1	1	4	16	52	82	88	63	33	23	16	13	3	2	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	42.56± .22	6.75± .16	15.85± .38
	C.A.	.....	1	4	5	10	25	52	94	80	58	38	19	12	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	42.65± .18	5.29± .12	12.64± .30
	C.F.	.....	.....	.....	.....	.....	3	11	27	76	86	86	43	39	18	6	3	1	1	.....	.....	.....	.....	.....	.....	.....	50.04± .19	5.67± .14	11.33± .27
8M	P.A.	.....	.....	.....	4	27	54	86	90	69	39	22	6	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	41.30± .18	5.44± .13	13.19± .31
	O.A.	1	3	16	29	30	50	68	87	62	31	15	7	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.91± .23	6.85± .16	17.16± .41
	C.A.	.....	.....	4	13	28	85	106	85	36	29	7	3	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.36± .18	5.46± .13	13.85± .33
	C.F.	1	5	10	28	40	57	58	72	60	34	21	11	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.73± .24	7.14± .17	17.97± .43
8N	O.A.	.....	.....	3	21	48	76	70	66	51	29	14	11	6	3	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.37± .23	6.48± .16	17.50± .41
	C.A.	.....	.....	8	14	30	73	91	90	46	25	12	6	2	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	39.73± .20	5.97± .14	15.03± .32
	C.F.	.....	.....	1	5	10	40	54	74	76	57	43	18	10	8	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	42.56± .18	5.48± .14	12.88± .31
8P	P.A.	.....	.....	.....	1	5	19	44	85	79	70	53	26	11	3	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	45.53± .20	5.98± .18	13.13± .31
	O.A.	.....	.....	.....	1	4	7	17	24	32	51	62	58	52	36	16	17	9	6	1	3	1	1	1	0	1	53.22± .31	9.40± .27	17.66± .32
	C.A.	.....	1	10	22	35	70	98	80	41	24	13	5	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	38.89± .20	5.94± .14	15.27± .39
	C.F.	.....	.....	.....	1	3	24	59	73	68	64	41	33	21	9	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	45.71± .22	6.65± .16	14.55± .34
8Q	P.A.	.....	.....	5	18	55	91	91	68	27	25	14	5	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	38.86± .19	5.74± .13	14.77± .34
	O.A.	1	3	12	19	38	46	53	69	59	33	29	22	9	3	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	41.32± .27	8.02± .19	19.41± .23
	C.F.	.....	.....	.....	4	11	12	41	45	73	60	53	45	37	13	3	3	.....	.....	.....	.....	.....	.....	.....	.....	.....	47.31± .25	7.29± .18	15.41± .37

8I—*P. faberi* from Florida 8L—*P. palmivora* from Porto Rico 8N—*P. palmivora* from India 8Q—*P. terrestris* from Florida
8K—*P. faberi* from Philippinnes 8M—*P. faberi* from Jamaica 8P—*P. palmivora* from Jamaica

*P.A.—Potato dextrose agar. O.A.—Oat meal agar. C.A.—Corn meal agar. C.F.—Corn meal flour.

TABLE V.—Variations and Constants for Widths of 400 Conidia of Strains of *Phytophthoras* Grown on Various Media Under Uniform Environmental Conditions.

Strains	Media or Environmental Conditions	Spore Classes According to Widths in Microns											Mean	Constants	
		13.35	16.49	19.63	22.77	25.91	29.05	32.19	35.33	38.47	41.61	44.75 47.89		Standard Deviation	Coefficient of Variability
8I	Potato dextrose agar			7	40	126	136	70	17	4			28.18± .12	3.49± .08	12.38± .29
	Oat meal agar			6	64	139	96	58	29	8			27.27± .14	3.85± .09	13.82± .33
	Corn meal agar		9	79	146	118	41	7					23.19± .12	3.65± .09	15.74± .38
	Corn meal flour		1	19	78	152	107	35	8				26.55± .11	3.40± .08	12.81± .31
8K	Potato dextrose agar		1	6	47	99	143	79	19	6			28.41± .12	3.68± .09	12.95± .29
	Oat meal agar				2	9	43	113	116	84	28	3 2	34.88± .13	3.97± .09	11.38± .28
	Corn meal agar	1	1	36	142	119	63	32	5	1			25.34± .12	3.67± .09	14.48± .34
	Corn meal flour				2	26	92	142	102	30	6		32.43± .12	3.46± .08	10.70± .25
8L	Potato dextrose agar			4	45	208	125	15	3				27.45± .11	3.19± .08	11.63± .28
	Oat meal agar		2	38	137	133	66	17	5	2			25.16± .12	3.49± .08	13.49± .32
	Corn meal agar			3	14	66	132	103	56	20	5	1	30.60± .14	4.02± .10	13.14± .31
	Corn meal flour				6	52	177	114	43	8			30.31± .10	3.06± .07	10.01± .24
8M	Potato dextrose agar			2	24	95	143	97	28	10	1		29.00± .12	3.65± .09	12.59± .30
	Oat meal agar		7	26	57	117	113	54	21	3	1	1	27.20± .15	4.36± .08	16.03± .38
	Corn meal agar		1	8	79	176	80	46	7	3			26.75± .11	3.27± .08	12.22± .29
	Corn meal flour	1	2	18	69	102	118	60	26	4			27.64± .14	4.19± .10	15.19± .36
8N	Oat meal agar		1	13	85	129	94	55	18	5			27.20± .14	4.07± .10	14.96± .35
	Corn meal agar		1	9	43	128	137	61	20	1			27.95± .12	3.53± .08	12.64± .30
	Corn meal flour			2	53	153	133	46	11	1	1		27.58± .11	3.17± .08	11.49± .28
8P	Potato dextrose agar				10	65	164	110	39	11	1		30.15± .11	3.28± .08	10.88± .27
	Oat meal agar			3	17	113	171	80	16				28.70± .10	2.91± .07	10.14± .24
	Corn meal agar		3	46	148	134	56	13					24.60± .11	3.13± .08	12.72± .30
	Corn meal flour			2	33	131	153	58	15	7	1		28.09± .11	3.30± .08	11.39± .28
8Q	Potato dextrose agar		2	8	76	136	105	43	22	7	1		27.66± .14	4.08± .10	14.75± .35
	Oat meal agar	1	6	25	50	94	74	67	46	28	8	1	32.06± .19	5.66± .14	17.65± .42
	Corn meal flour			10	30	84	98	106	46	24	1	1	33.01± .15	4.54± .10	13.75± .32

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8N—*P. palmivora* from India
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

TABLE VI.—Variations and Constants for Diameters of 400 Chlamydospores of Strains of *Phytophthoras*.

Strains	Media or Environmental Conditions	Spore Classes According to Diameters in Microns														Constants		
		16.49	19.63	22.77	25.91	29.05	32.19	35.33	38.47	41.61	44.75	47.89	51.03	54.17	57.31	60.45	Mean	Standard Deviation	Coefficient of Variability
8I	Potato dex. agar	.....	3	22	62	80	86	80	39	23	4	1	.....	.....	.....	.....	31.95± .18	5.23± .13	16.37± .39
	Oat meal agar	2	8	18	57	84	93	67	43	23	4	1	.....	.....	.....	.....	32.19± .18	5.41± .13	13.86± .33
	Corn meal flour	.....	4	8	21	41	94	108	82	32	9	1	.....	.....	.....	.....	34.31± .16	4.84± .12	14.16± .34
8K	Potato dex. agar	.....	2	13	15	51	57	65	79	57	43	13	2	2	1	.....	36.26± .21	6.31± .15	17.40± .42
	Oat meal agar	.....	4	7	17	28	42	73	85	68	43	16	9	4	3	1	37.87± .21	6.30± .15	16.64± .39
	Corn meal flour	.....	.....	3	11	15	21	43	65	100	73	30	22	10	7	.....	41.04± .22	6.57± .16	16.01± .34
8L	Potato dex. agar	.....	4	9	31	45	78	96	75	41	14	5	2	.....	.....	.....	34.66± .19	5.55± .13	16.01± .38
	Oat meal agar	.....	1	3	27	57	113	116	58	20	4	1	.....	.....	.....	.....	33.17± .14	4.02± .10	15.14± .36
	Corn meal flour	.....	.....	4	24	58	118	132	49	10	4	1	.....	.....	.....	.....	33.47± .13	3.94± .09	11.75± .28
8M	Potato dex. agar	4	18	47	74	93	81	54	21	5	3	.....	.....	.....	.....	.....	28.00± .14	4.07± .10	14.54± .35
	Oat meal agar	.....	.....	4	10	15	47	80	104	87	39	10	4	.....	.....	.....	37.89± .17	5.06± .12	13.35± .32
	Corn meal flour	.....	4	13	44	71	82	74	57	40	13	2	.....	.....	.....	.....	33.39± .19	5.66± .14	16.95± .39
8P	Potato dex. agar	2	.....	5	15	67	103	109	58	29	6	2	.....	.....	.....	.....	30.89± .15	4.56± .11	14.76± .36
	Oat meal agar	1	.....	3	8	44	76	93	96	57	15	4	1	.....	.....	.....	32.75± .16	4.74± .11	14.47± .34
	Corn meal flour	.....	.....	2	5	19	33	75	110	93	47	14	2	.....	.....	.....	35.38± .16	4.83± .12	9.21± .23
8Q	Potato dex. agar	3	.....	13	43	101	108	66	33	19	11	3	.....	.....	.....	.....	28.14± .17	5.13± .12	17.64± .42
	Oat meal agar	.....	.....	1	6	21	45	74	83	76	52	23	10	6	3	.....	35.97± .20	5.99± .14	16.65± .39
	Corn meal flour	.....	.....	.....	3	16	36	62	99	79	51	32	17	4	1	.....	36.72± .19	5.66± .13	15.41± .37

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

TABLE VII.—Summary of Differences in the Mean Dimensions of Conidia of 7 Strains Belonging to 3 Species of *Phytophthora* Grown on 4 Different Culture Media Under Uniform Environmental Conditions.

Substratum	Strains Compared	Differences in Means (in Microns)		Differences in Means Divided by Probable Error of the Differences	
		Length	Width	Length	Width
Potato dextrose agar	8P and 8I	6.40±.29	1.97± .16	22.17	12.31
Potato dextrose agar	8P and 8K	4.95± .29	1.74± .16	17.07	10.88
Potato dextrose agar	8P and 8L	6.53± .25	2.70± .16	26.12	16.88
Potato dextrose agar	8P and 8M	4.23± .28	1.15± .16	18.39	6.56
Potato dextrose agar	8P and 8Q	6.67± .28	2.49± .18	24.18	13.83
Potato dextrose agar	8P and 8I	2.17± .28	.82± .17	7.75	4.82
Potato dextrose agar	8P and 8K	.72± .28	.59± .17	2.64	3.49
Potato dextrose agar	8P and 8L	2.30± .24	1.55± .16	9.58	9.69
Potato dextrose agar	8P and 8Q	2.44± .26	1.34± .18	9.39	7.44
Potato dextrose agar	8K and 8I	1.45± .30	.23± .17	4.83	1.30
Potato dextrose agar	8K and 8L	1.57± .26	.96± .16	6.08	6.00
Potato dextrose agar	8K and 8Q	1.52± .28	.75± .18	5.43	4.17
Potato dextrose agar	8I and 8L	.13± .29	.73± .16	.45	4.56
Potato dextrose agar	8I and 8Q	.27± .28	.52± .18	.96	2.89
Potato dextrose agar	8L and 8Q	.14± .24	.21± .18	.58	1.17
Oat meal agar	8P and 8I	10.84± .43	.52± .16	25.21	3.25
Oat meal agar	8P and 8K	1.21± .41	6.18± .16	2.95	3.63
Oat meal agar	8P and 8L	10.66± .38	3.54± .16	28.53	22.13
Oat meal agar	8P and 8M	13.31± .39	1.50± .18	34.13	8.33
Oat meal agar	8P and 8N	13.89± .39	.50± .17	36.90	8.82
Oat meal agar	8P and 8Q	12.90± .41	3.36± .21	31.46	16.00
Oat meal agar	8I and 8K	11.05± .33	7.61± .19	33.48	40.05
Oat meal agar	8I and 8L	.82± .34	3.02± .17	2.41	17.77
Oat meal agar	8I and 8M	3.47± .38	.98± .19	9.13	5.16
Oat meal agar	8I and 8N	4.01± .38	.98± .18	15.53	5.44
Oat meal agar	8I and 8Q	2.06± .40	3.88± .22	5.02	18.00
Oat meal agar	8L and 8M	2.65± .32	2.04± .19	8.28	10.70
Oat meal agar	8L and 8N	3.19± .32	2.04± .18	9.97	11.33
Oat meal agar	8L and 8Q	1.24± .35	6.90± .25	3.54	27.60
Oat meal agar	8L and 8K	11.89± .34	9.72± .20	34.97	48.50
Oat meal agar	8Q and 8K	13.11± .38	2.82± .23	34.50	12.26
Oat meal agar	8Q and 8M	1.41± .35	4.86± .24	4.03	20.25
Oat meal agar	8Q and 8N	1.95± .35	4.86± .26	5.57	18.46
Oat meal agar	8N and 8K	14.52± .35	7.60± .20	41.48	38.00
Oat meal agar	8N and 8N	.54± .33	.00± .00	1.64	.00
Oat meal agar	8N and 8K	15.06± .35	7.68± .19	43.03	40.42

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8N—*P. palmivora* from India
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

TABLE VII.—Summary of Differences in the Mean Dimensions of Conidia of 7 Strains Belonging to 3 Species of *Phytophthora* Grown on 4 Different Culture Media Under Uniform Environmental Conditions.—Continued.

Substratum	Strains Compared	Differences in Means (in Microns)		Differences in Means Divided by Probable Error of the Differences	
		Length	Width	Length	Width
Corn meal agar	8L and 8I	6.27± .27	7.41± .18	23.22	41.17
Corn meal agar	8L and 8K	5.99± .25	5.11± .18	23.96	28.28
Corn meal agar	8L and 8M	3.29± .25	3.85± .18	13.16	21.39
Corn meal agar	8L and 8N	2.92± .25	2.65± .18	11.68	14.72
Corn meal agar	8L and 8P	3.76± .27	6.00± .18	13.93	33.33
Corn meal agar	8N and 8I	5.27± .27	4.76± .17	19.52	28.00
Corn meal agar	8N and 8K	5.90± .25	2.64± .17	23.60	15.53
Corn meal agar	8N and 8M	.37± .27	1.20± .16	1.37	7.50
Corn meal agar	8N and 8P	.84± .28	3.35± .16	3.00	21.94
Corn meal agar	8M and 8I	2.97± .27	2.56± .16	11.07	16.00
Corn meal agar	8M and 8K	2.70± .25	1.41± .16	10.80	8.81
Corn meal agar	8M and 8P	.47± .27	2.15± .15	1.74	14.33
Corn meal agar	8P and 8I	2.51± .28	1.41± .16	8.96	8.81
Corn meal agar	8P and 8K	2.23± .27	1.26± .16	8.63	7.88
Corn meal agar	8I and 8K	.28± .27	2.15± .17	1.04	12.65
Corn meal flour	8L and 8I	6.93± .29	3.76± .15	23.90	25.07
Corn meal folur	8L and 8K	.51± .33	2.12± .16	1.55	13.25
Corn meal flour	8L and 8M	10.31± .26	1.57± .17	33.22	9.23
Corn meal flour	8L and 8N	7.48± .26	2.73± .20	28.77	13.65
Corn meal flour	8L and 8P	4.33± .29	2.22± .15	14.97	14.80
Corn meal flour	8L and 8Q	2.73± .31	2.70± .18	8.81	15.00
Corn meal flour	8Q and 8I	4.20± .36	6.46± .19	11.67	34.00
Corn meal flour	8Q and 8K	3.24± .38	.58± .19	8.53	3.05
Corn meal flour	8Q and 8M	7.54± .35	5.37± .20	21.54	26.86
Corn meal flour	8Q and 8N	4.75± .31	5.43± .19	15.32	28.53
Corn meal flour	8Q and 8P	1.60± .33	4.92± .19	4.85	25.89
Corn meal flour	8P and 8I	2.60± .34	2.54± .16	7.65	15.88
Corn meal flour	8P and 8K	4.84± .35	4.34± .16	13.83	27.12
Corn meal flour	8P and 8M	5.98± .32	.45± .20	18.69	2.25
Corn meal flour	8P and 8N	3.15± .28	.51± .16	11.25	3.19
Corn meal flour	8I and 8K	7.44± .38	5.88± .16	19.32	36.75
Corn meal flour	8I and 8M	3.38± .35	1.09± .20	9.66	5.45
Corn meal flour	8I and 8N	.55± .32	1.03± .16	1.72	6.44
Corn meal flour	8N and 8K	7.99± .33	4.85± .16	24.21	30.31
Corn meal flour	8N and 8M	2.83± .30	.06± .20	9.43	.30
Corn meal flour	8M and 8K	10.82± .36	4.76± .18	30.06	26.44

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8N—*P. palmivora* from India
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

TABLE VIII.—Summary of Differences in the Mean Diameters of Chlamydospores of 6 Strains Belonging to 3 *Phytophthora* Species Grown on 3 Different Culture Media Under Uniform Environmental Conditions.

Strains Compared	Potato Dextrose Agar — Diameter: Difference in Means (in Microns)	Potato Dextrose Agar — Diameter: Difference Divided by Probable Error	Strains Compared	Oat Meal Agar — Diameter: Difference in Means (in Microns)	Oat Meal Agar — Diameter: Difference Divided by Probable Error	Strains Compared	Corn Meal Flour — Diameter: Difference in Means (in Microns)	Corn Meal Flour — Diameter: Difference Divided by Probable Error
8K and 8L	1.66± .28	5.93	8M and 8K	.02± .27	.07	8K and 8Q	4.32± .24	14.90
8K and 8I	4.31± .28	15.39	8M and 8Q	1.91± .26	7.35	8K and 8P	5.66± .27	20.96
8K and 8P	6.37± .26	24.50	8M and 8L	4.72± .22	21.45	8K and 8I	6.73± .27	24.93
8K and 8Q	7.12± .27	26.37	8M and 8P	3.24± .23	14.09	8K and 8L	7.59± .26	29.12
8K and 8M	8.24± .25	33.04	8M and 8I	5.70± .25	22.80	8K and 8M	7.64± .29	26.38
8L and 8I	2.71± .26	10.42	8K and 8Q	1.90± .29	6.55	8Q and 8P	1.34± .25	5.36
8L and 8P	3.77± .24	15.71	8K and 8L	4.70± .25	18.80	8Q and 8I	2.41± .25	9.64
8L and 8Q	5.54± .25	27.16	8K and 8P	5.14± .26	19.77	8Q and 8L	3.25± .23	14.13
8L and 8M	6.66± .24	27.75	8K and 8I	5.68± .28	20.29	8Q and 8M	3.33± .27	12.33
8I and 8P	1.06± .23	4.61	8Q and 8L	2.80± .24	11.67	8P and 8I	1.07± .23	4.65
8I and 8Q	2.81± .25	11.24	8Q and 8P	3.22± .26	12.39	8P and 8L	1.89± .21	9.09
8I and 8M	3.95± .23	17.17	8Q and 8I	3.78± .27	14.00	8P and 8M	1.99± .25	7.96
8P and 8Q	1.75± .23	7.61	8L and 8P	.42± .21	2.00	8I and 8L	.84± .21	4.00
8P and 8M	2.89± .21	13.76	8L and 8I	.97± .23	4.70	8I and 8M	.92± .25	3.68
8Q and 8M	1.14± .22	5.02	8P and 8I	.56± .24	2.33	8L and 8M	.08± .23	.35

8I—*P. faberi* from Florida
8K—*P. faberi* from Philippines
8L—*P. palmivora* from Porto Rico
8M—*P. faberi* from Jamaica
8P—*P. palmivora* from Jamaica
8Q—*P. terrestris* from Florida

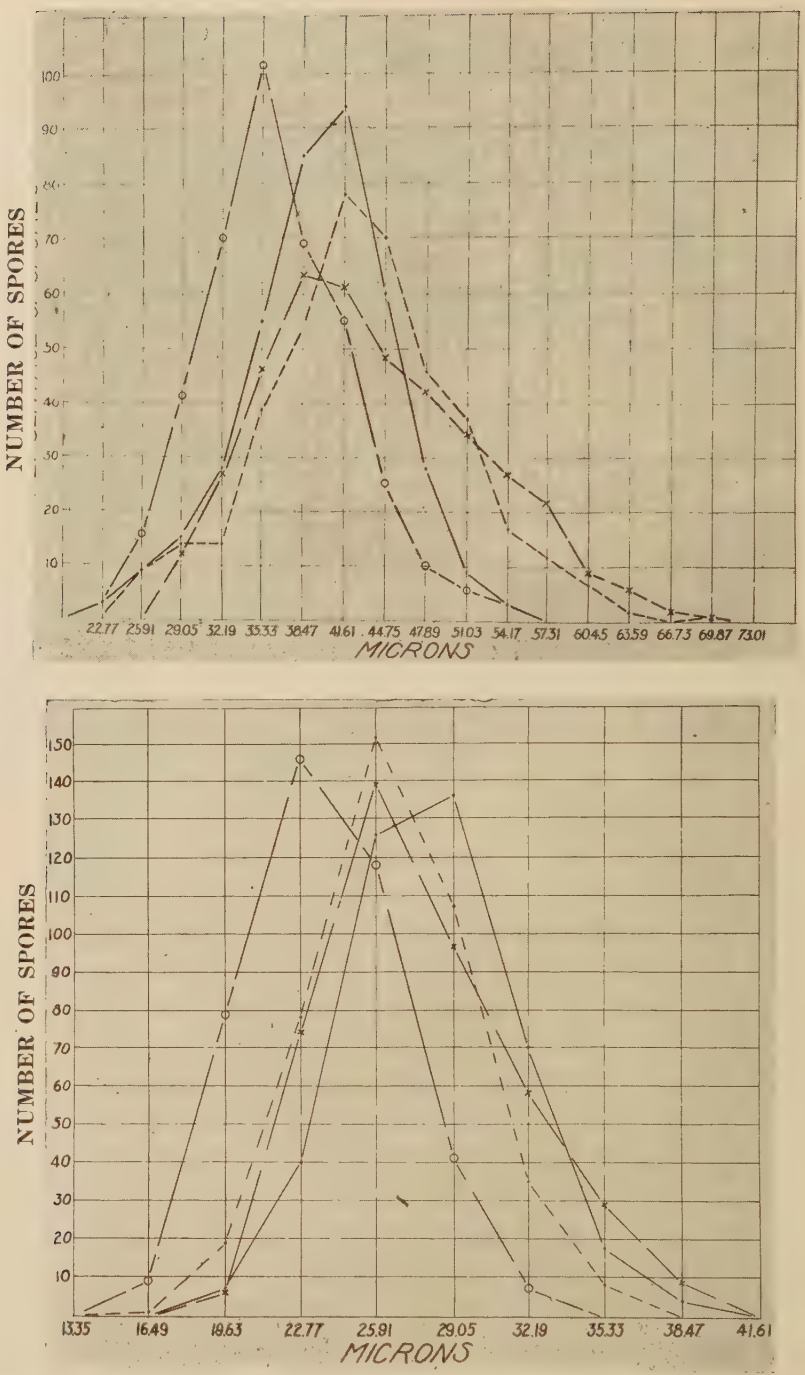

Fig. 22.—Curves showing the differences in length (upper) and width (lower) of conidia of strain 8I when grown on various culture media under uniform cultural conditions. .——. Potato dextrose agar, mean length 39.13± 0.21, mean width 28.18± 0.12; x——x Oatmeal agar, mean length 43.38± 0.30, mean width 27.27± 0.14; o——o Corn meal agar, mean length 36.38± 0.20, mean width 23.19± 0.12; .- - - . Corn meal flour, mean length 43.11± 0.26, mean width 26.55± 0.11.

EFFECT OF DIFFERENT CULTURE MEDIA ON SPORE SIZE

As previously stated, no two workers seem to agree on the size of the conidia and chlamydospores produced by the various organisms which cause coconut bud rot. From the number of factors that might affect the size of the spore, one can readily see why this condition exists. The greatest variation occurs in the larger spore dimensions and is clearly shown by the effect of the media on spore length. There is also great variation in the diameter of the chlamydospores of the several strains of *Phytophthora* studied when cultured on three different media. In general, there is more variation in the diameter of chlamydospores than in the width of conidia, but less so than in their length.

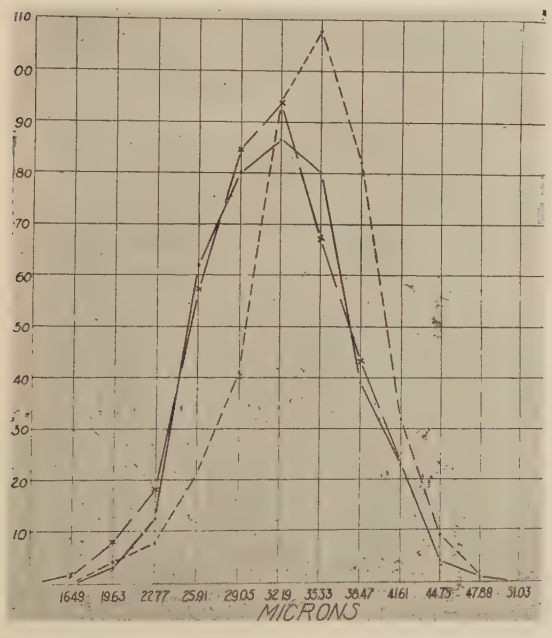

Fig. 23.—Curves showing the differences in diameters of chlamydospores of strain 8I when grown on various culture media under uniform cultural conditions. .——. Potato dextrose agar; mean diameter 31.95± 0.18. x——x, Oatmeal agar; mean diameter 32.19± 0.18. .- - - -. Corn meal flour; mean diameter 34.31± 0.16.

Phytophthora faberi from Florida (8I). — Conidia of this strain when produced on oatmeal agar averaged 7μ longer than those produced on corn meal agar. The narrowest as well as the shortest conidia were produced on the latter substrata. The broadest conidia, on the other hand, were produced on potato dextrose agar. There appeared to be a significant difference in the size of chlamydospores of strain 8I when grown on potato dextrose agar and corn meal agar and oatmeal agar, respectively.

Phytophthora faberi from the Philippines (8K).—In the case of strain 8K, as in the case of strain 8I, the longest conidia were

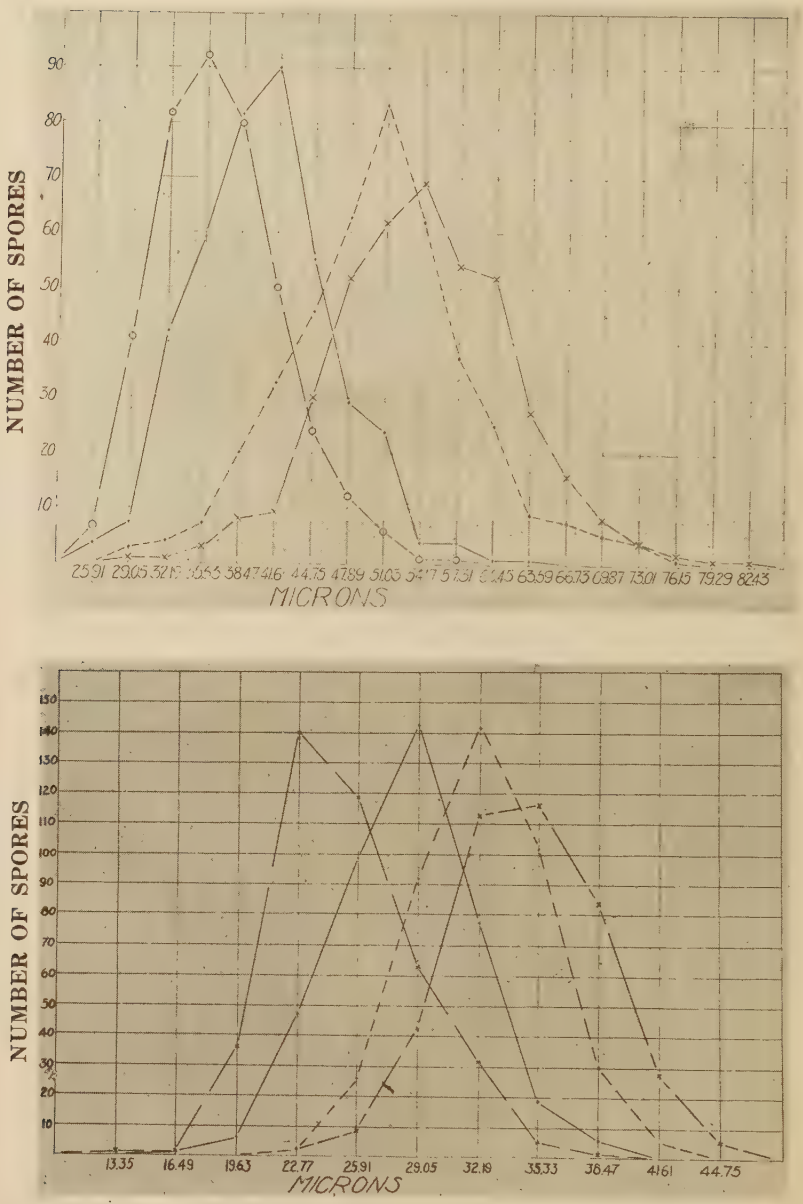

Fig. 24.—Curves showing the difference in length (upper) and width (lower) of conidia of strain 8K when grown on various cultural media under uniform cultural conditions. .——. On potato dextrose agar; mean length 40.58± 0.21. x— —x. Oatmeal agar; mean length 54.43± 0.26. o— — —o Corn meal agar; mean length 36.66± 0.18. . - - - . Corn meal flour; mean length 50.55± 0.27. .——. Potato dextrose agar; mean width 28.41± 0.12. x— — —x Oatmeal agar; mean width 34.88± 0.13. x— —x Corn meal agar; mean width 25.34± 0.12. - - - - . Corn meal flour; mean width 32.43± 0.12.

produced on oatmeal agar and the smallest ones on corn meal agar, but the difference in the mean length was 17.77μ, a difference of approximately 50 percent. Furthermore, unlike strain 8I the spore width of 8K was most favorably influenced by the same substrata as the latter's conidia length, i. e. by oatmeal agar. The narrowest conidia were produced on corn meal agar, on which the conidia of 8I were also the shortest. In the case of chlamydospores the largest spores were produced on corn meal flour, and the smallest ones on potato dextrose agar.

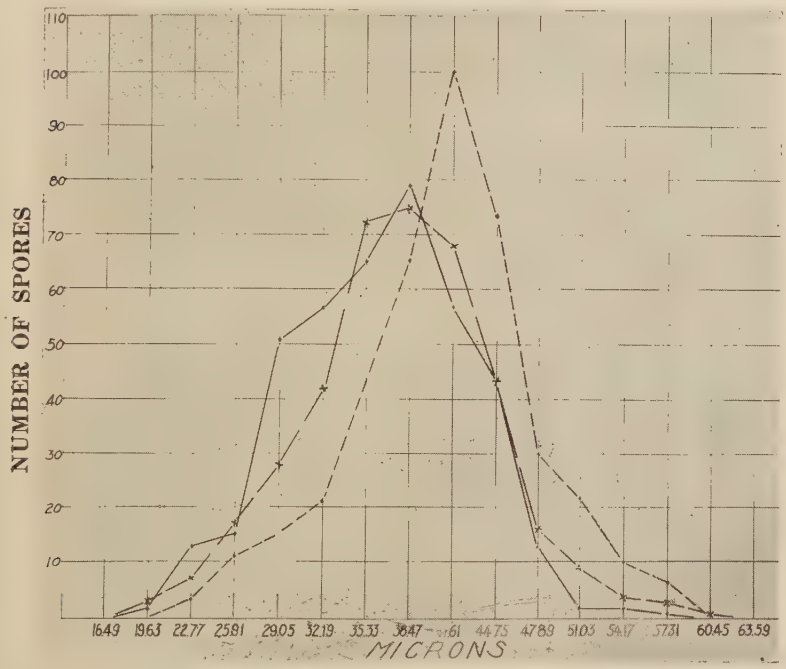

Fig. 25.—Differences in diameters of chlamydospores of strain 8K when grown on various culture media under uniform cultural conditions. .——., on potato dextrose agar; mean diameter 36.26± 0.21. x— —x, on oatmeal agar; mean diameter 37.87± 0.21. . - - - ., on corn meal flour; mean diameter 41.04± 0.22.

Phytophthora palmivora from Porto Rico (8L).—The conidia of this strain were shortest on potato dextrose agar and longest on corn meal flour. They were narrowest on oatmeal agar and widest on corn meal agar, although there was very little difference in width between those grown on corn meal agar and corn meal flour. The greatest difference in the chlamydospore size of this strain was noted on potato dextrose agar and oat-

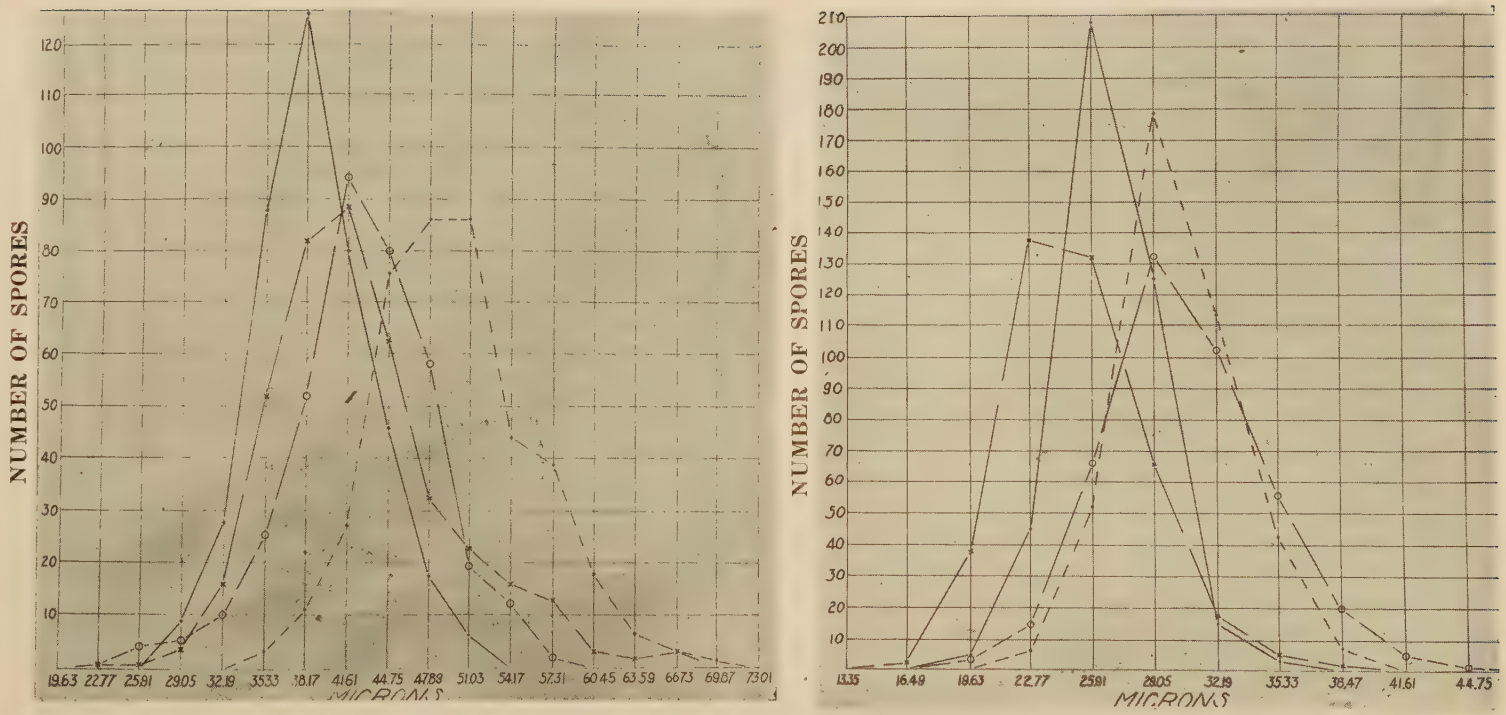

Fig. 26.—Curves showing the differences in length (left) and width (right) of conidia of strain 8L when grown on various culture media under uniform cultural conditions. .——., on potato dextrose agar; mean length 39.00 ± 0.15 x— —x, on oatmeal agar; mean length 42.56± 0.22. o— —o, on corn meal agar, mean length 42.65± 0.18. .- - -. on corn meal flour; mean length 50.04± 0.19. .——., on potato dextrose agar; mean width 27.45± 0.11 x— —x, on oatmeal agar; mean width 25.16± 0.12. o— —o, on corn meal agar; mean width 30.60± 0.14. .- - -., on corn meal flour; mean width 30.31± 0.10.

meal agar culture; the spores in the former media exceeding those in the latter by about 1.5μ.

Phytophthora faberi from Jamaica (8M).—There appeared to be very little variation in spore length of strain 8M on the different culture media. The variation was somewhat greater in the width of the conidia on the different media and in a few cases fairly significant. Very pronounced and undoubtedly highly significant differences appeared in the size of the chlamydospores of this strain when grown on different culture media. The difference was especially great between the chlamydospores produced on potato dextrose agar and oatmeal agar, a difference of almost 10μ in favor of the spores grown on the last named media.

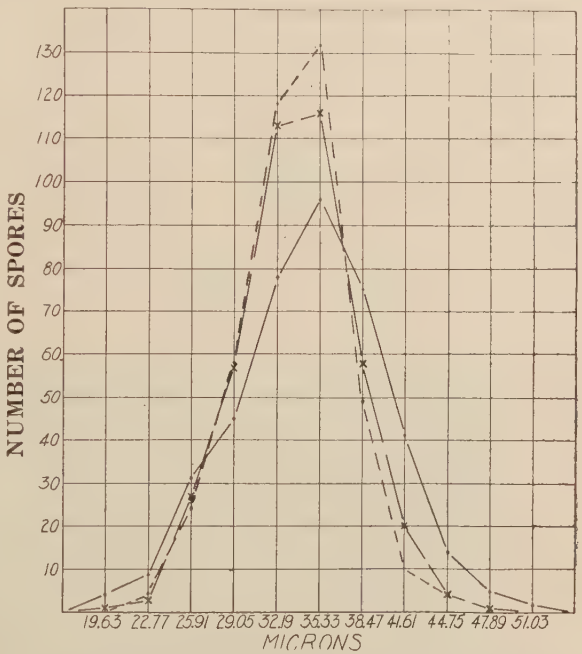

Fig. 27.—Differences in diameters of chlamydospores of strain 8L when grown on various culture media under uniform cultural conditions. .——., on potato dextrose agar; mean diameter 34.66± 0.19. x— —x, on oatmeal agar; mean diameter 33.17± 0.14. .- - - -., on corn meal flour; mean diameter 33.47± 0.13.

Phytophthora palmivora from India (8N).—The different media exerted considerable variation in the length of the conidia of this strain, the longest conidia being produced on corn meal flour and the shortest on oatmeal agar. Very little difference in length was noted on the conidia produced on oatmeal agar and corn meal agar. No great difference appeared in the conidia width of this strain on the different media. Unfortunately strain 8N did not yield sufficient conidia on potato dextrose agar to permit spore

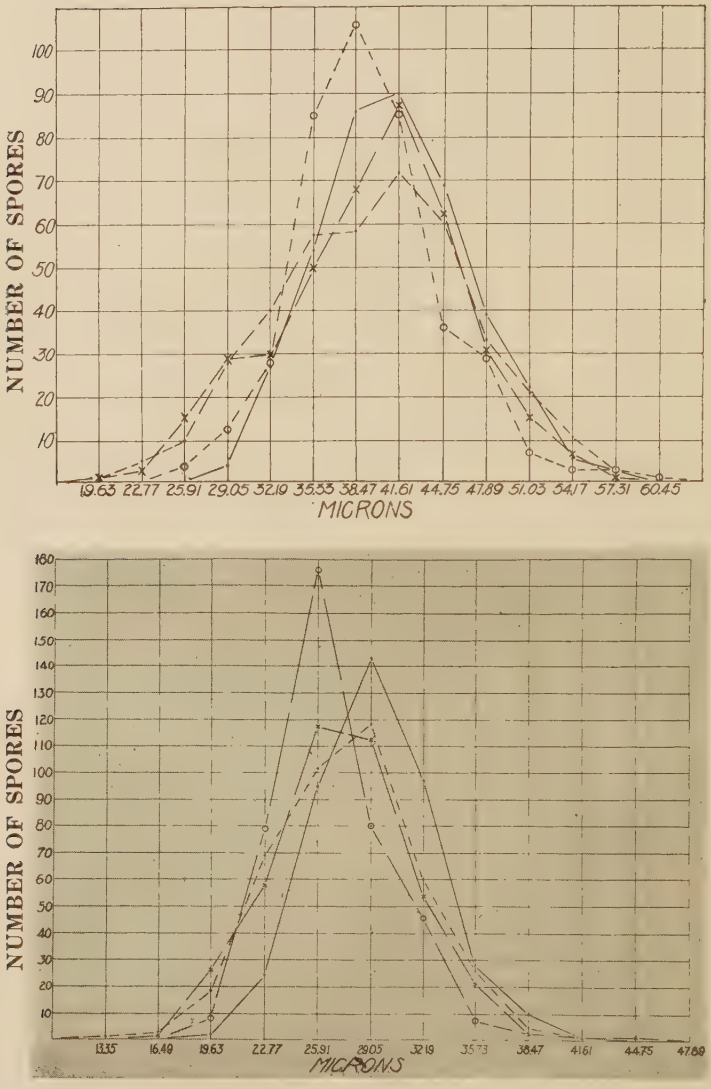

Fig. 28.—Curves showing the differences in length (upper) and width (lower) of conidia of strain 8M when grown on various culture media under uniform cultural conditions. .——., on potato dextrose agar; mean length 41.30± 0.18. x— —x, on oatmeal agar; mean length 39.91± 0.23. o— — —o, on corn meal agar; mean length 39.36± 0.18. . - - -, on corn meal flour; mean length 39.73± 0.24. .——., on potato dextrose agar; mean width 29.00± 0.12. x— —x, on oatmeal agar; mean width 27.20± 0.15. o— —o, on corn meal agar; mean width 26.75± 0.11. . - - -, on corn meal flour; mean width 27.64± 0.14.

measurement on this substrata. Likewise, no chlamydospores, or very few of them, were produced on any of the media of this strain.

Phytophthora palmivora from Jamaica (8P).—There was a marked effect on the size of conidia, both length and width, and

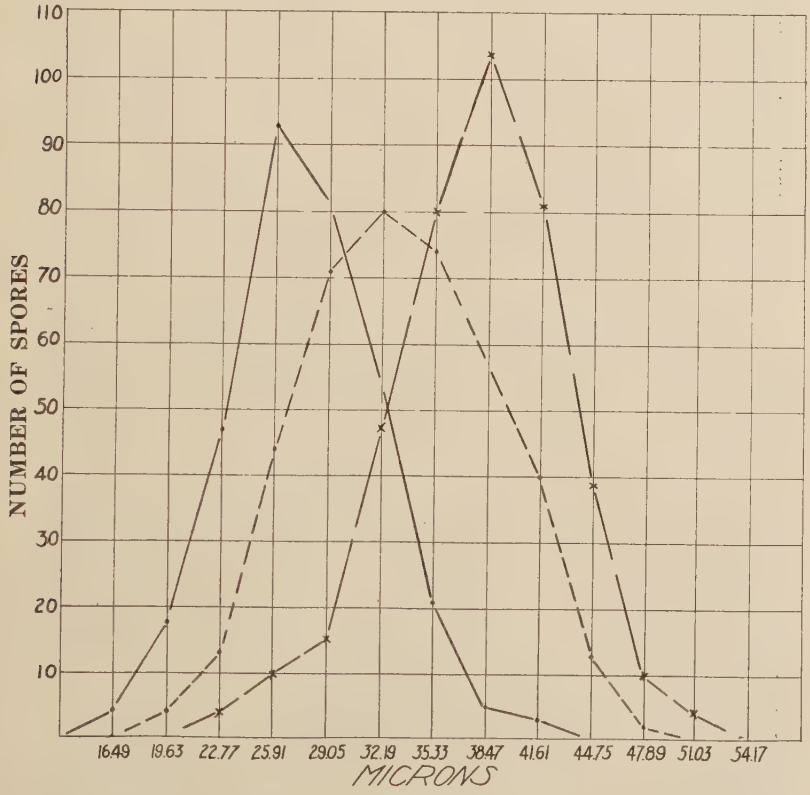

Fig. 29.—Differences in diameters of chlamydospores of strain 8M when grown on various culture media under uniform cultural conditions. .——., on potato dextrose agar; mean diameter 28.00± 0.14. x— —x on oatmeal agar; mean diameter 37.89± 0.17. . - - ., on corn meal flour; mean diameter 33.39± 0.19.

on the diameter of the chlamydospores of this strain, by the different culture media used. The effect was very similar in this case to that produced by the substrata on the spores of strain 8K, except that in the present case the greatest difference in the mean length of the conidia was about 30 percent, whereas in the case of 8K it was approximately 50 percent.

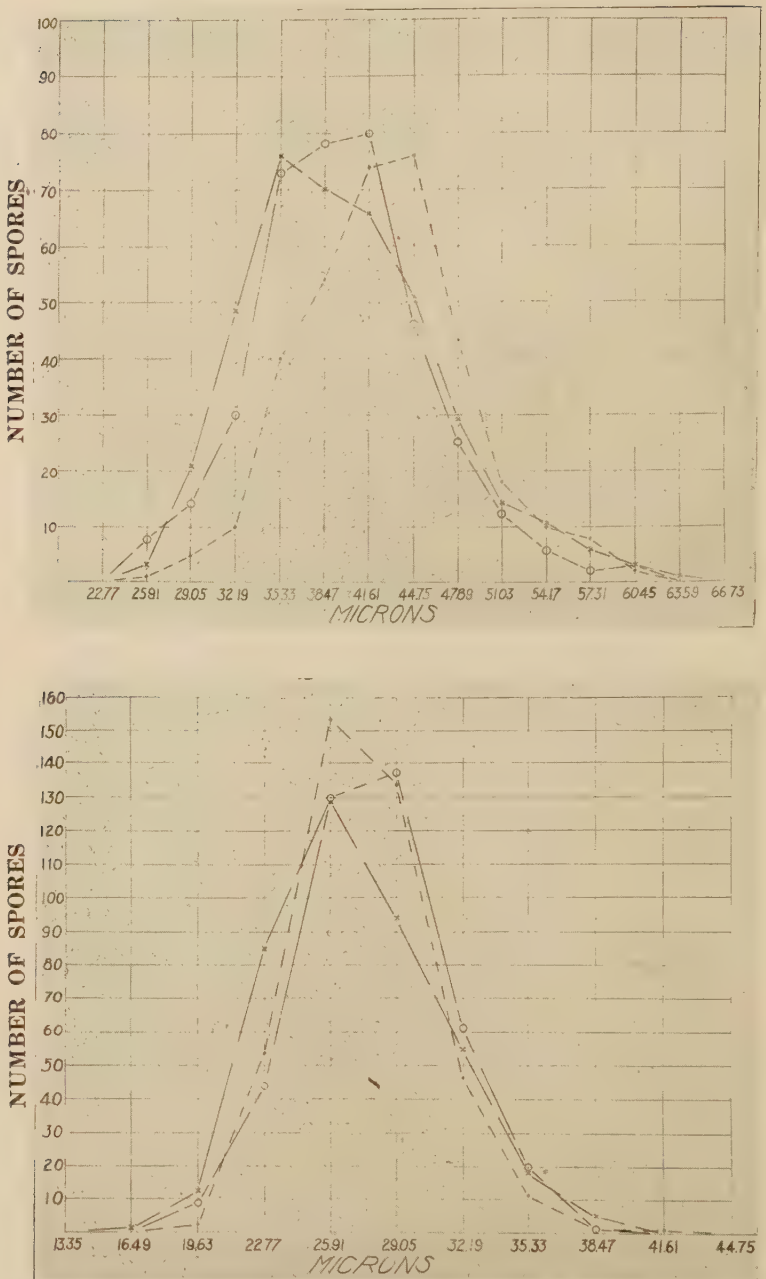

Fig. 30.—Curves showing the differences in length (above) and width (below) of conidia of strain 8N when grown on various culture media under uniform cultural conditions. x— —x oatmeal agar; mean length 39.37± 0.23. o— —o, corn meal agar; mean length 39.73± 0.20. .— — —., corn meal flour; mean length 42.56± 0.18. x— —x, oatmeal agar; mean width 27.20± 0.14. o— —o, corn meal agar; mean width 27.95± 0.12. .— — —., corn meal flour; mean width 27.58± 0.11.

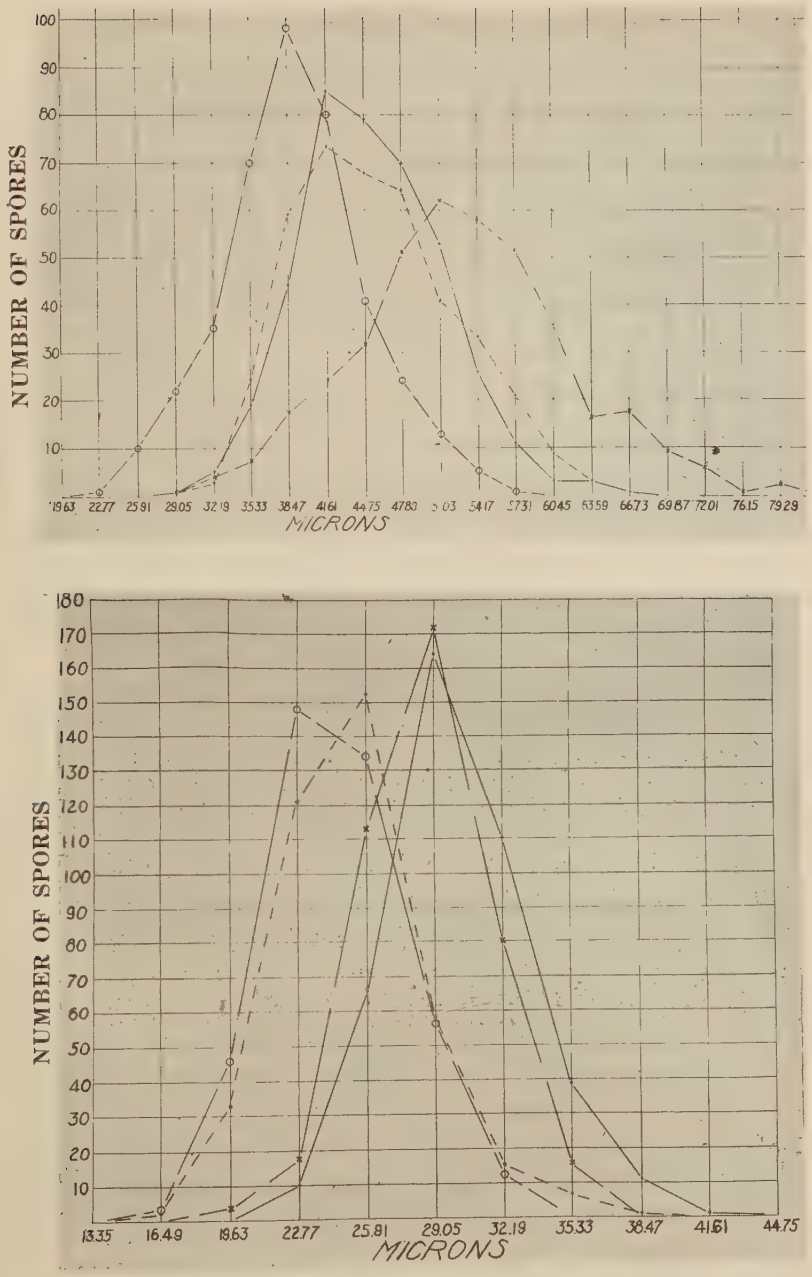

Fig. 31.—Curves showing the differences in length (above) and width (below) of conidia of strain 8P when grown on various cultural media under uniform cultural conditions .——., potato dextrose agar; mean length 45.54± 0.20. x— —x, oatmeal agar; mean length 53.22± 0.31. o- - -o, corn meal agar; mean length 38.89± 0.20. . - - - . corn meal f.our; mean length 45.71± 0.22. .——., potato dextrose agar; mean width 30.15± 0.11. x— —x oatmeal agar; mean width 28.70± 0.10. o— —o, corn meal agar; mean width 24.60± 0.11. o— —o, corn meal flour; mean width 28.09± 0.10.

Phytophthora terrestris from Florida (8Q).—A very large variation in spore size of this organism occurred on the different media. Both conidia and chlamydospores were affected by

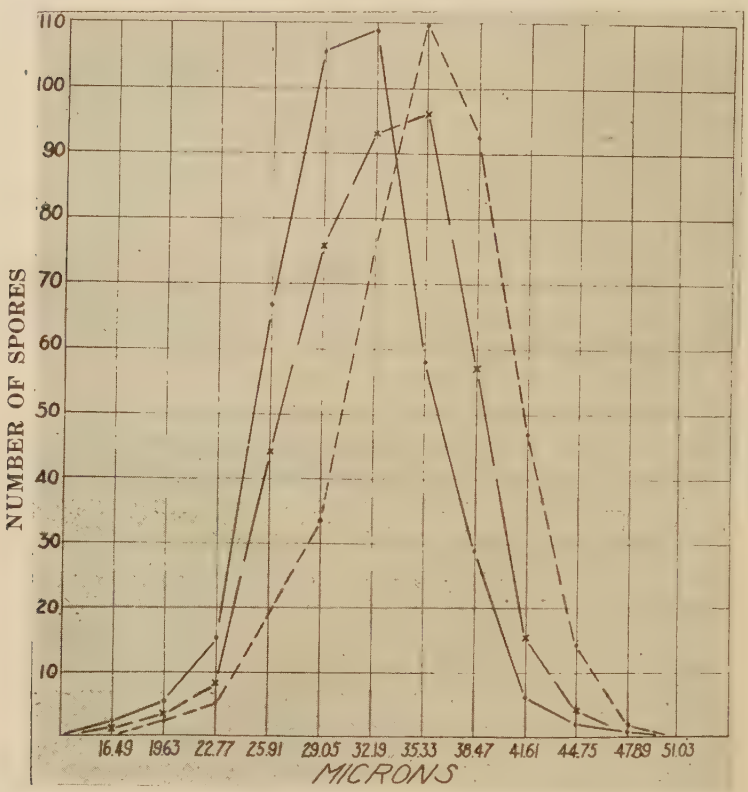

Fig. 32.—Differences in diameter of chlamydospores of strain 8P when grown on various culture media under uniform cultural conditions. .——. potato dextrose agar; mean diameter 30.89± 0.15. x— —x, oatmeal agar; mean diameter 32.75± 0.16. .- - - corn meal flour; mean diameter 35.38± 0.16.

the culture media. Corn meal flour yielded the longest conidia and potato dextrose agar the shortest. The same was true regarding the width of the conidia and the diameter of the chlamydospores.

COMPARATIVE SIZE OF SPORES OF DIFFERENT STRAINS ON THE SAME MEDIA

In order to determine whether or not the different species and strains of *phytophthora* studied differ from each other in a sig-

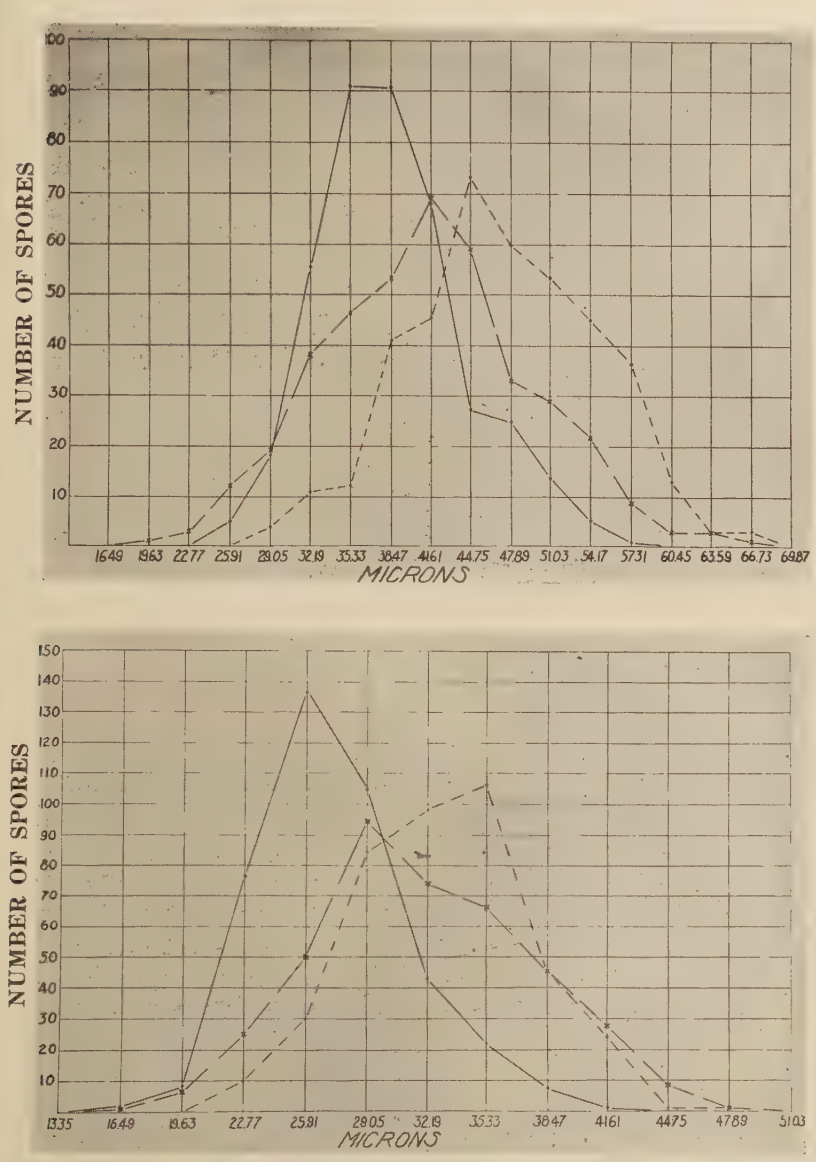

Fig. 33.—Curves showing the differences in length (above) and width (below) of conidia of strain 8Q when grown on various culture media under uniform cultural conditions. .——., potato dextrose agar; mean length 38.86± 0.19. x— —x, oatmeal agar, mean length 41.32± 0.27. . - - - ., corn meal flour; mean length 47.31± 0.25. .——, potato dextrose agar; mean width 27.66± 0.14. x— —x, oat meal agar; mean width 32.06± 0.19. . - - - corn meal flour; mean width 33.01± 0.15.

nificant way as far as the size of the conidia and chlamydospores are concerned, various strains were cultured on different culture media under virtually identical environmental conditions. Comparisons were made between cultures of the different strains grown on the same media and of the same stage of development.

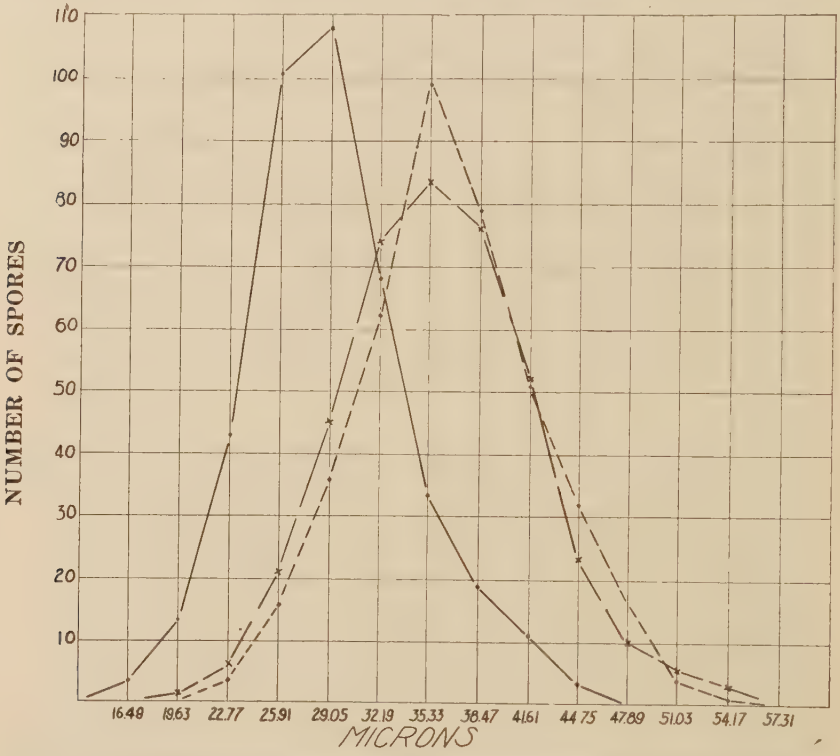

Fig. 34.—Differences in diameters of chlamydospores of strain 8Q when grown on various culture media under uniform cultural conditions. .——., potato dextrose agar; mean diameter 28.14± 0.17. x— —x, oatmeal agar; mean diameter 35.97± 0.20. . - - - ., corn meal flour; mean diameter 36.72± 0.19.

The results are recorded in Tables VII and VIII, and illustrated in figures 35 to 41. A more or less detailed discussion of the results obtained follows:

On Potato Dextrose Agar.—Significant differences in both length and width of conidia occurred on potato dextrose agar. The difference was very pronounced in both dimensions and appeared to be statistically significant. The greatest difference was noted in the conidial length of strains 8P and 8Q, the former exceeding the latter by 6.67± 0.28μ. In the case of conidia width

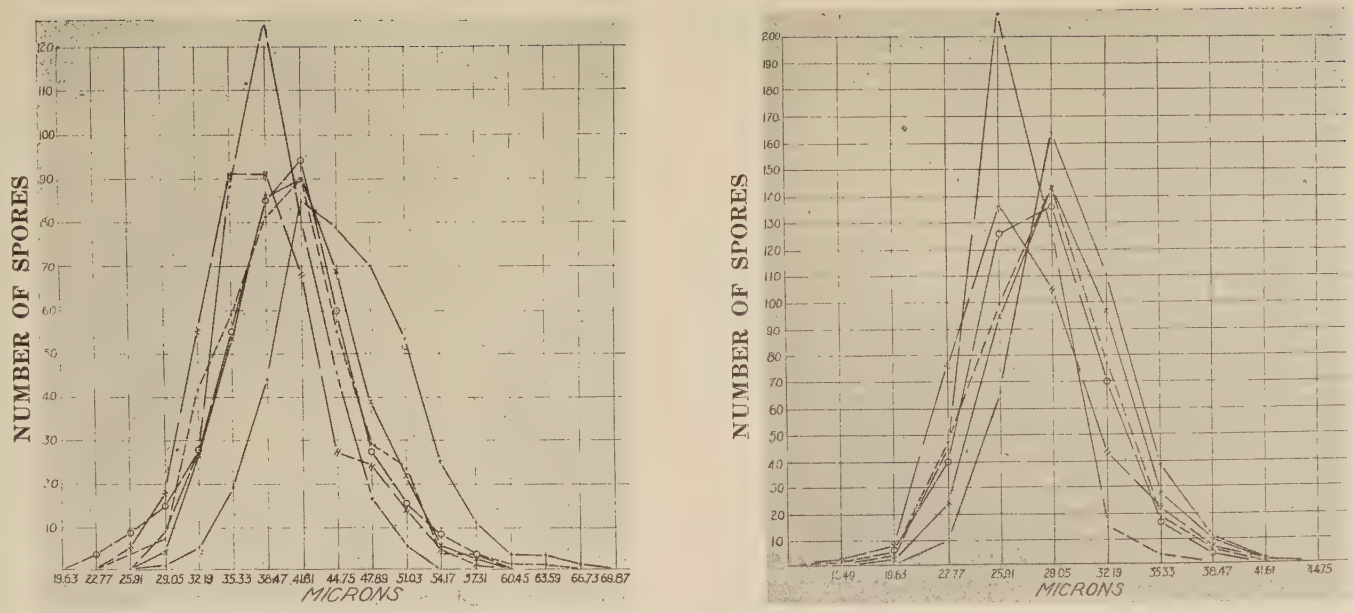

Fig. 35.—Curves showing the differences in length (left) and width (right) of conidia of various Phytophthora strains when grown on potato dextrose agar under uniform cultural conditions. o— —o, strain 8I; mean length 39.13± 0.21. . - - - ., strain 8K; mean length 40.58± 0.21. .— — —., strain 8M; mean length 41.30± 0.18. .——., strain 8P; mean length 45.53± 0.20. 1:1——1:1, strain 8Q; mean length 38.86± 0.13. o— —o, strain 8I; mean width 28.18± 0.12. - - - strain 8K; mean width 28.41± 0.12. .— — —., strain 8L; mean width 27.45± 0.11. x——x strain 8M; mean width 29.00± 0.12. .——., strain 8P; mean width 30.15± 0.11. 1:1——1:1, strain 8Q; mean width 27.66± 0.14.

the greatest difference occurred between strains 8P and 8L, amounting to 2.70± 0.16μ in favor of 8P. By far the largest chlamydospores in this experiment were produced by strain 8K and the smallest ones by strain 8M. Strains 8I, 8L and 8Q were practically identical as far as conidial length is concerned; and there was hardly any difference in conidial width of strains 8I and 8K on the one hand and 8L and 8Q on the other hand. More

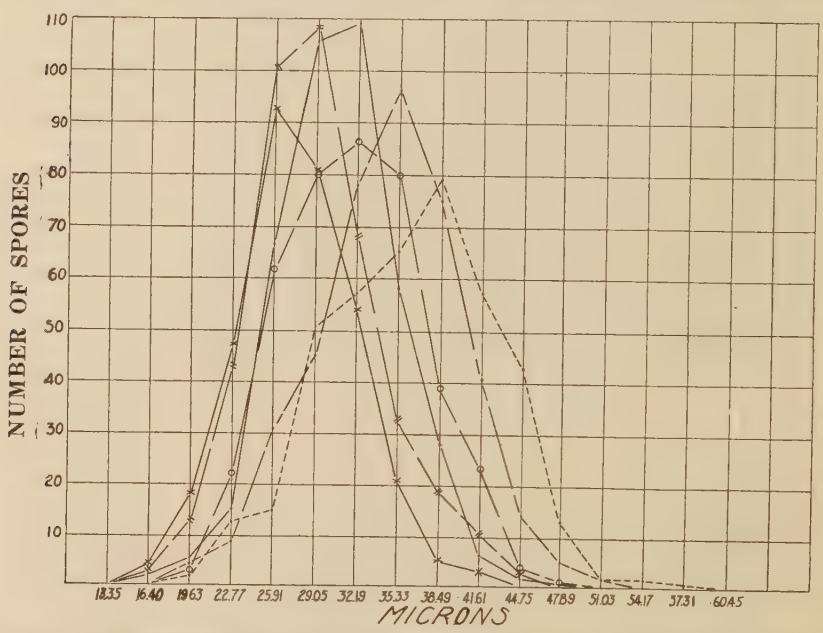

Fig. 36.—Differences in diameters of chlamydospores of the various Phytophthora strains when grown on potato dextrose agar under uniform cultural conditions. o— —o, strain 8I; mean diameter 31.95± 0.18. .- - -., strain 8K; mean diameter 36.26± 0.21. .- — -., strain 8L; mean diameter 34.66± 0.19. x——x, strain 8M; mean diameter 28.00± 0.14. .———., strain 8P; mean diameter 30.89± 0.15. 1:1—1:1, strain 8Q; mean diameter 29.14± 0.17.

or less significant differences prevailed between the chlamydospores of the various strains when cultured on potato dextrose agar.

On Oatmeal Agar.—The greatest difference in length, but not in the width, of conidia of the *Phytophthora* causing bud rot occurred when they were cultured on oatmeal agar. As great a difference as 15.06± 0.35μ occurred between strains 8N and 8K; 8K having the longest conidia on this media. The latter strain had the broadest conidia, while 8L had the narrowest ones, with a difference of 9.72± 0.20μ. Strain 8K shared the honor of hav-

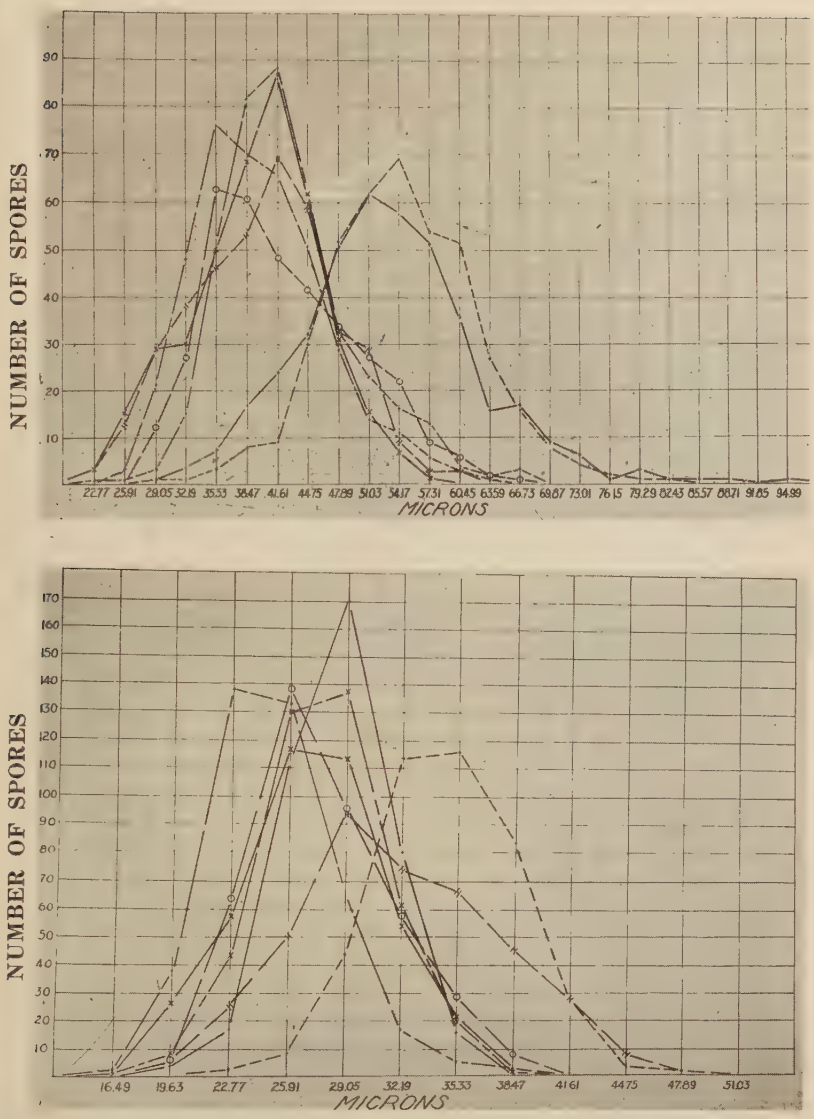

Fig. 37.—Curves showing the differences in length (above) and width (below) of conidia of various Phytophthora strains when grown on oatmeal agar under uniform cultural conditions. o— —o, strain 8I; mean length 43.38± 0.30. .- - -., strain 8K; mean length 54.43± 0.26. .- — -., strain 8L; mean length 42.56± 0.22. x——x, strain 8M; mean length 39.91± 0.23. .— - —, strain 8N; mean length 39.37± 0.23. .———., strain 8P; mean length 53.22± 0.31. 1:1——1:1, strain 8Q; mean length 38.86± 0.19. o— —o, strain 8I; mean width 27.27± 0.14. . - - - ., strain 8K; mean width 34.88± 0.13. .- — -, strain 8L; mean width 25.16± 0.12. x——x strain 8M; mean width 27.20± 0.15. x— - —x, strain 8N; mean width 27.95± 0.12. .——., strain 8P; mean width 28.70± 0.10. 1:1—1:1, strain 8Q; mean width 32.06± 0.19.

ing the largest chlamydospores on oatmeal agar with strain 8M. The chlamydospores of these two strains were practically identical. Strain 8I had the smallest chlamydospores of all, but not significantly smaller than those of strain 8P.

On Corn Meal Agar.—The greatest difference between the conidial length of any two strains of coconut bud rotting organisms grown on corn meal agar occurred between strains 8I and

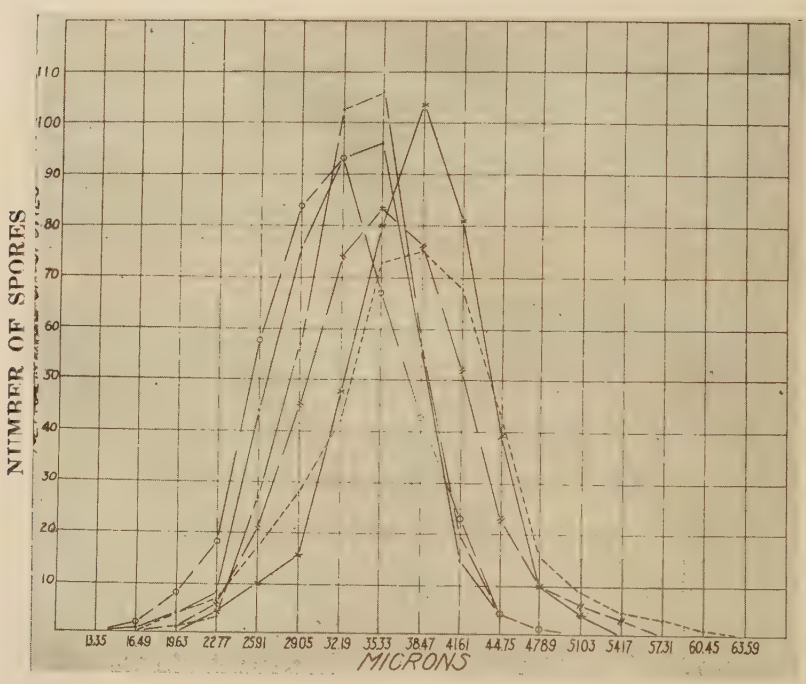

Fig. 38.—Differences in the diameter of the chlamydospores of the various Phytophthora strains when grown on oatmeal agar under uniform cultural conditions. o——o, strain 8I; mean diameter 32.19± 0.18. .---., strain 8K; mean diameter, 37.87± 0.14. .-——-., strain 8L; mean diameter, 33.17± 0.14. x——x, strain 8M; mean diameter 37.89± 0.17. .——., strain 8P; mean diameter 32.75± 0.16. 1:1——1:1 strain 8Q; mean diameter 36.72± 0.19.

8L, with a difference of 6.27± 0.27μ in favor of strain 8L. However, this difference must be considered as highly significant statistically, since it exceeds its probable error by more than 23 times. Strain 8L had not only the longest but also the widest conidia, and, similarly, strain 8I had both the shortest and the narrowest conidia. The difference in the conidial width of these

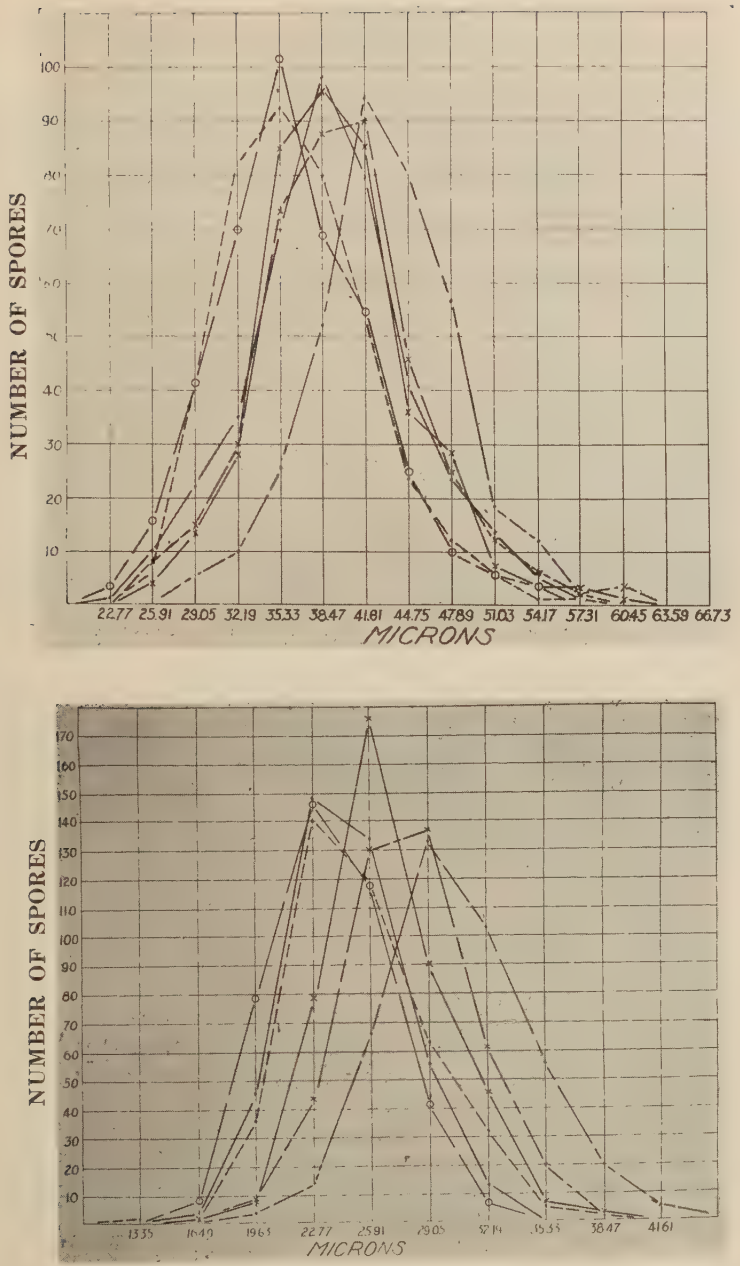

Fig. 39.—Curves showing the differences in length (above) and width (below) of conidia of various Phytophthora strains when grown on corn meal agar under uniform cultural conditions. o— —o, strain 8I; mean length 36.38± 0.20. .- - -. strain 8K; mean length 36.66± 0.18. .— — -., strain 8L; mean length 42.65± 0.18. x——x., strain 8M; mean length 39.36± 0.18. x— — —x, strain 8N; mean length 39.73± 0.20. .——., strain 8P; mean length 38.89± 0.20. o— —o, strain 8I; mean width 23.19± 0.12. .- - -., strain 8K; mean width 25.34± 0.12. . — — — ., strain 8L; mean width 30.60± 0.14. x——x, strain 8M; mean width 26.75± 0.11. x— — —x., strain 8N; mean width 27.95± 0.12. . ——., strain 8P; mean width 24.60± 0.11.

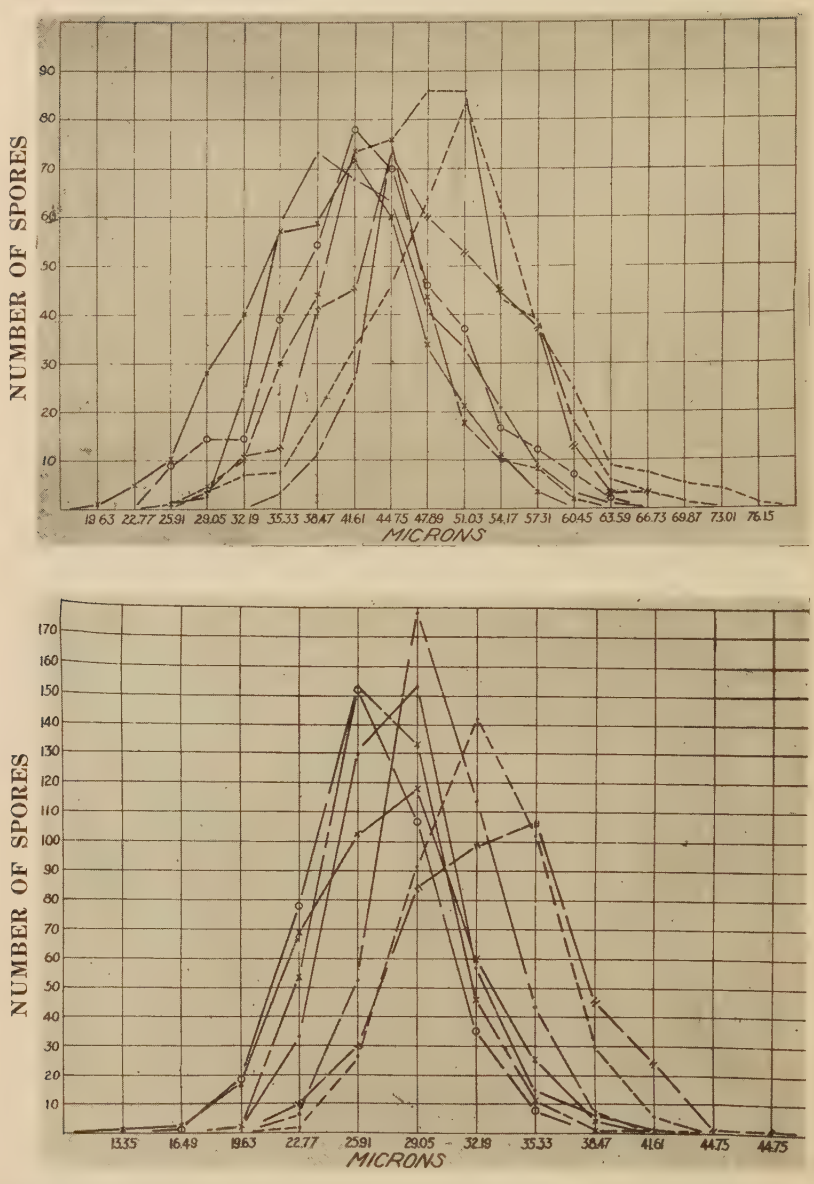

Fig. 40.—Curves showing the differences in length (above) and width (below) of conidia of various Phytophthora strains when grown on corn meal flour under uniform cultural conditions. o— —o, strain 8I; mean length 43.11± 0.17. .- - -., strain 8K; mean length 50.55± 0.19. .— — —., strain 8L; mean length 50.04± 0.19. x——x, strain 8M; mean length 39.73± 0.24. x— —x, strain 8N; mean length 42.56± 0.18. .——, strain 8P; mean length 47.75± 0.22. 1:1—1:1, strain 8Q; mean length 47.31± 0.25. o— —o, strain 8I; mean width 26.55± 0.11. .- - -., strain 8K; mean width 32.43± 0.12. .— — —., strain 8L; mean width 30.31± 0.10. x——x, strain 8M; mean width 27.64± 0.14. x— — —x, strain 8N; mean width 27.58± 0.11. .——., strain 8P; mean width 28.09± 0.11. 1:1—1:1, strain 8Q; mean width 33.01± 0.15.

two strains was even greater and certainly much more significant than the difference in their length.

On Corn Meal Flour.—The longest conidia on corn meal flour were produced by strain 8K, while the shortest ones were

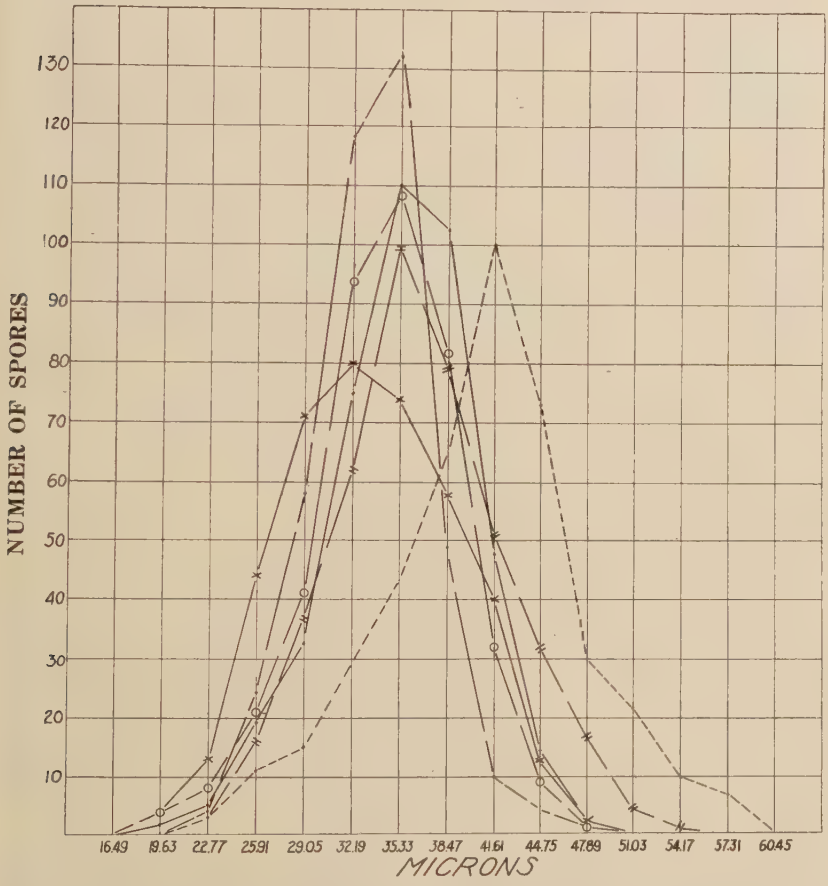

Fig. 41—Differences in diameters of chlamydospores of the various Phytophthora strains when grown on corn meal flour under uniform cultural conditions. o— —o, strain 8I; mean diameter 34.31± 0.16. .- - -., strain 8K; mean diameter 41.04± 0.22. .— — —., strain 8L; mean diameter 33.67± 0.13. x——x., strain 8M; mean diameter 33.39± 0.19. .——., strain 8P; mean diameter 35.38± 0.16. 1:1——1:1, strain 8Q; mean diameter 36.72± 0.19.

produced by strain 8M. There was a difference of 10.82± 0.36μ between the two, which on the face of it is a very significant difference. Strain 8Q possessed the widest conidia on this culture media, while strain 8I had the narrowest, with a difference of 6.46± 0.19μ between them. Besides having the longest con-

idia, strain 8K also had the largest chlamydospores. Conversely, 8M had the smallest chlamydospores as well as the shortest conidia. The difference in the chlamydospore size of strain 8M and 8L was both actually and statistically insignificant.

An analysis of Tables VII and VIII will show that, on each and every one of the cultural media, significant differences in the length and width of conidia and diameter of chlamydospores occurred between the individual strains of *Phytophthora* causing bud rot. On potato dextrose agar, *P. palmivora* from Jamaica, strain 8P, differed definitely from every one of the other strains; however, on oatmeal agar it was difficult to distinguish this strain, on the basis of conidial length, from *P. faberi* from the Philippines, strain 8K. However, these two strains differed very pronouncedly in conidial width and in chlamydospore size. In other cases strain 8P was similar to, or practically identical with, other strains in conidial width, yet differing significantly from these strains either in conidial length or chlamydospore size, or both. On neither of the other two media was there any one strain that could always be distinguished from all the other strains on the basis of spore size alone.

LENGTH TO WIDTH RATIO

Spore shape has been used as a means of separating Linean species of *Phytophthora* and biologic forms of *P. graminis*. Rosenbaum *(29)* points out that length to width ratios are constant characters. It is obvious that this method of expression gives a more complete picture of spore morphology, and, when used along with other characters, is a more useful method of comparison.

Effect of Substratum on Conidial Shape of the Different Strains.—Even a superficial study of figures 30-35 will show what a striking effect cultural media has on the shape of *Phytophthora* conidia. This is but normal, since on different media, frequently, only one diameter of the conidia is affected by the substrata; thereby changing the morphogenic processes of the spores. The effect of the media was by no means consistent, as some strains produced a greater quantity of more or less round conidia on one media while other strains would have more or less elongated spores on the same media, and vice versa.

Characteristic Conidial Shape of the Different Strains.—Not only could certain of the strains of *Phytophthora* studied

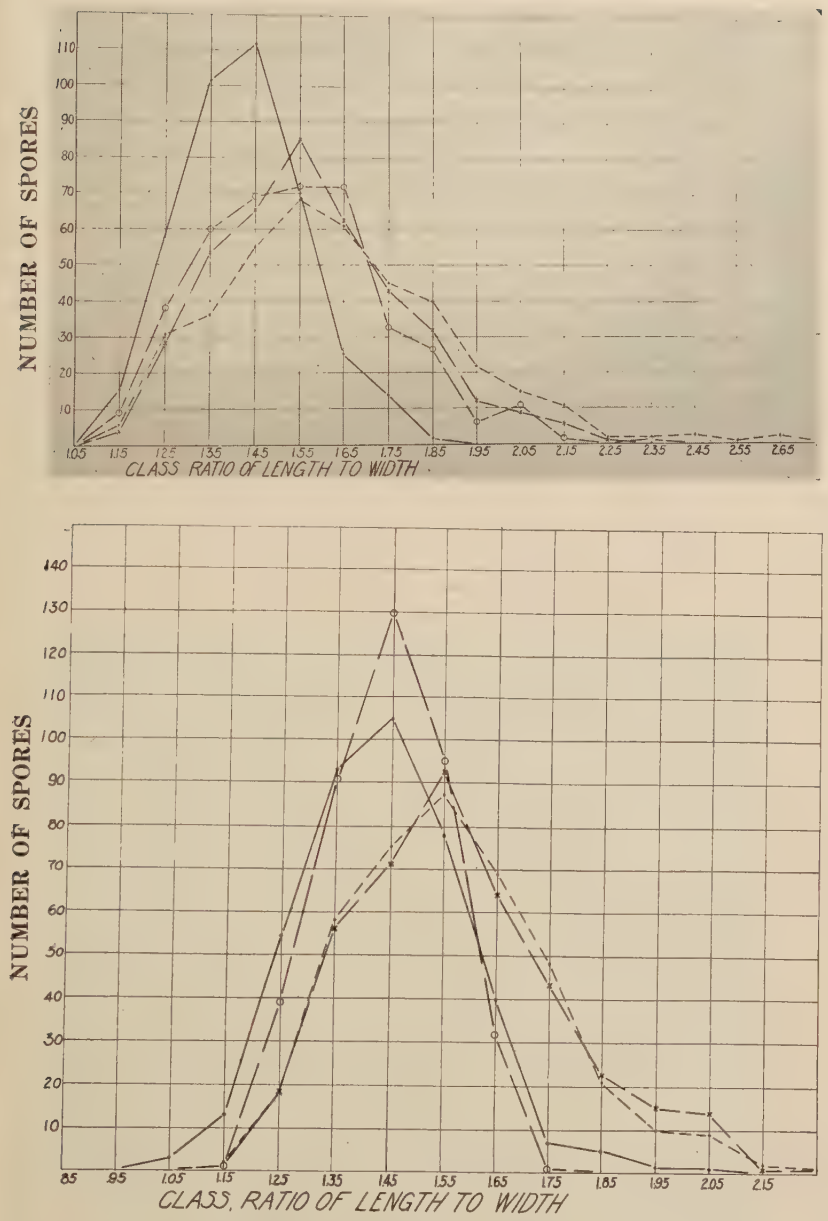

Fig. 42.—Curves showing the differences in ratio of lengths to widths of strain 8I (above) and strain 8K (below) when grown on different culture media under uniform cultural conditions. .——., on potato dextrose agar; x— —x, on oatmeal agar; o— —— —o, on corn meal agar; .- - -., on corn meal flour.

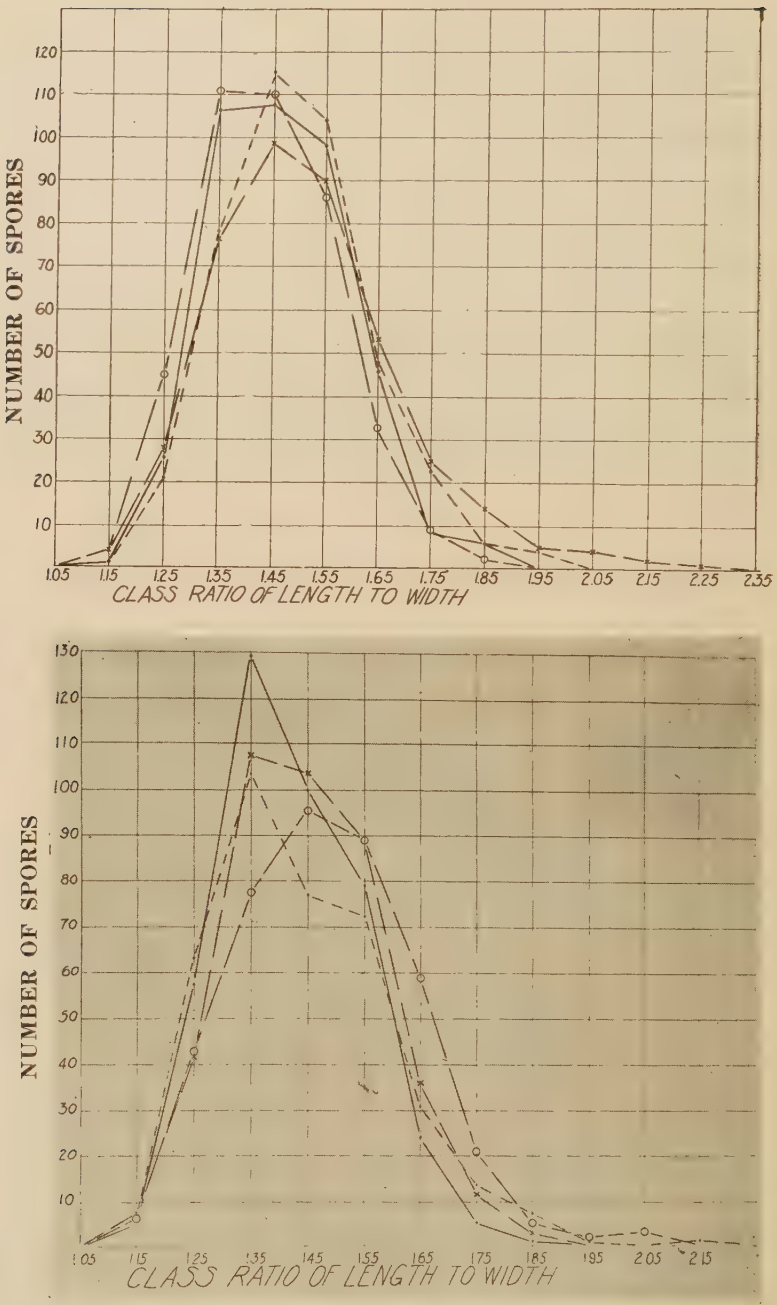

Fig. 43.—Curves showing the difference in ratio of lengths to widths of strain 8L (above) and strain 8M (below) when grown on different cultural media under uniform cultural conditions. .——., potato dextrose agar; x— —x, on oatmeal agar; o— —o, on corn meal agar; . - - -, on corn meal flour.

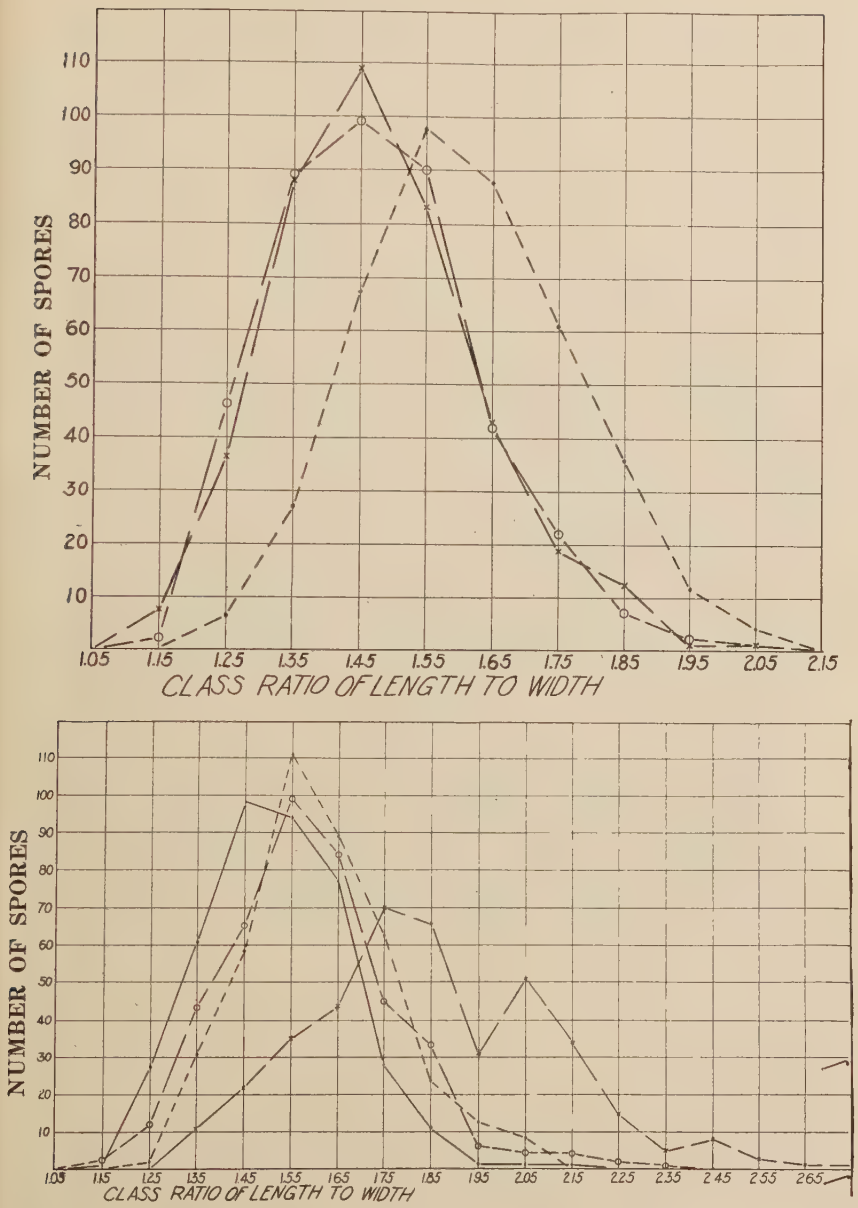

Fig. 44.—Curves showing the differences in ratio of lengths to widths of strain 8N (above) and strain 8P (below) when grown on different culture media under uniform cultural conditions. .——., on potato dextrose agar; x— —x, on oatmeal agar; o— — —o, on corn meal agar; .- - -, on corn meal flour.

be differentiated on the basis of spore size differences, but also on the basis of the prevailing conidial shape when produced on certain congenial media. Thus, for example, the conidia of the strain 8P were predominately ellipsoid in shape when cultured on oat meal agar, whereas strain 8M and 8Q had a great many spheroidal conidia. On corn meal agar, on the other hand, it is strains 8I and 8P that may be characterized by more or less

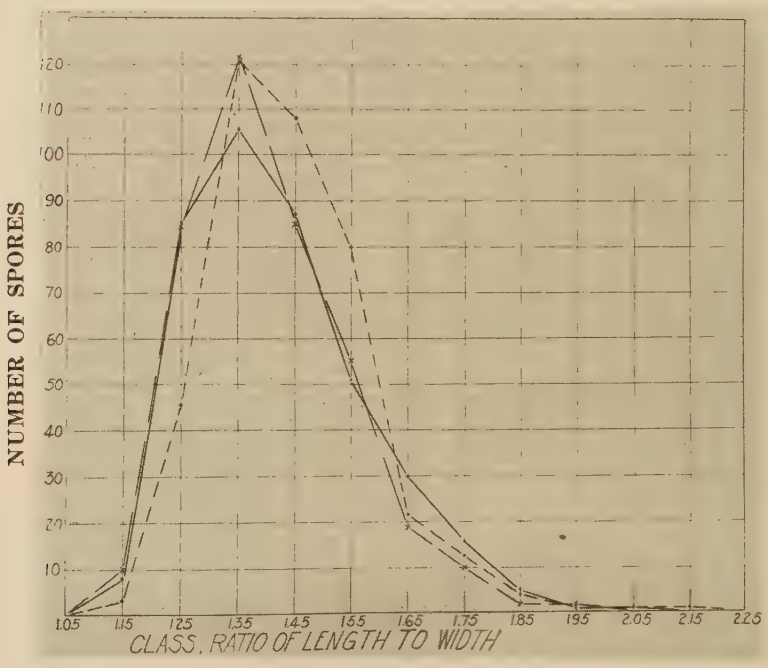

Fig. 45.—Differences in ratio of lengths to widths of conidia of strain 8Q when grown on various media under uniform cultural conditions. .——., on potato dextrose agar; x— —x, on oatmeal agar; .- - -., on corn meal flour.

ellipsoidal conidia, while strain 8L has rather predominately spheroidal conidia.

Ashby *(2)* finds that young conidia of P. *palmivora* grown on corn meal flour have a ratio of length to width of 1.75:1—1.77:1, whereas old conidia have a ratio of 1.52:1—1.57:1. Conidia from a leaf of the host has a ratio of 1.55:1 and from the host a ratio of 1.61:1. Rosenbaum *(29)* gives a mean ratio for this organism of 1.47:1, while Reinking *(28)* find a ratio of 1.60:1 when the organism is grown on oatmeal agar and 1.51:1 when

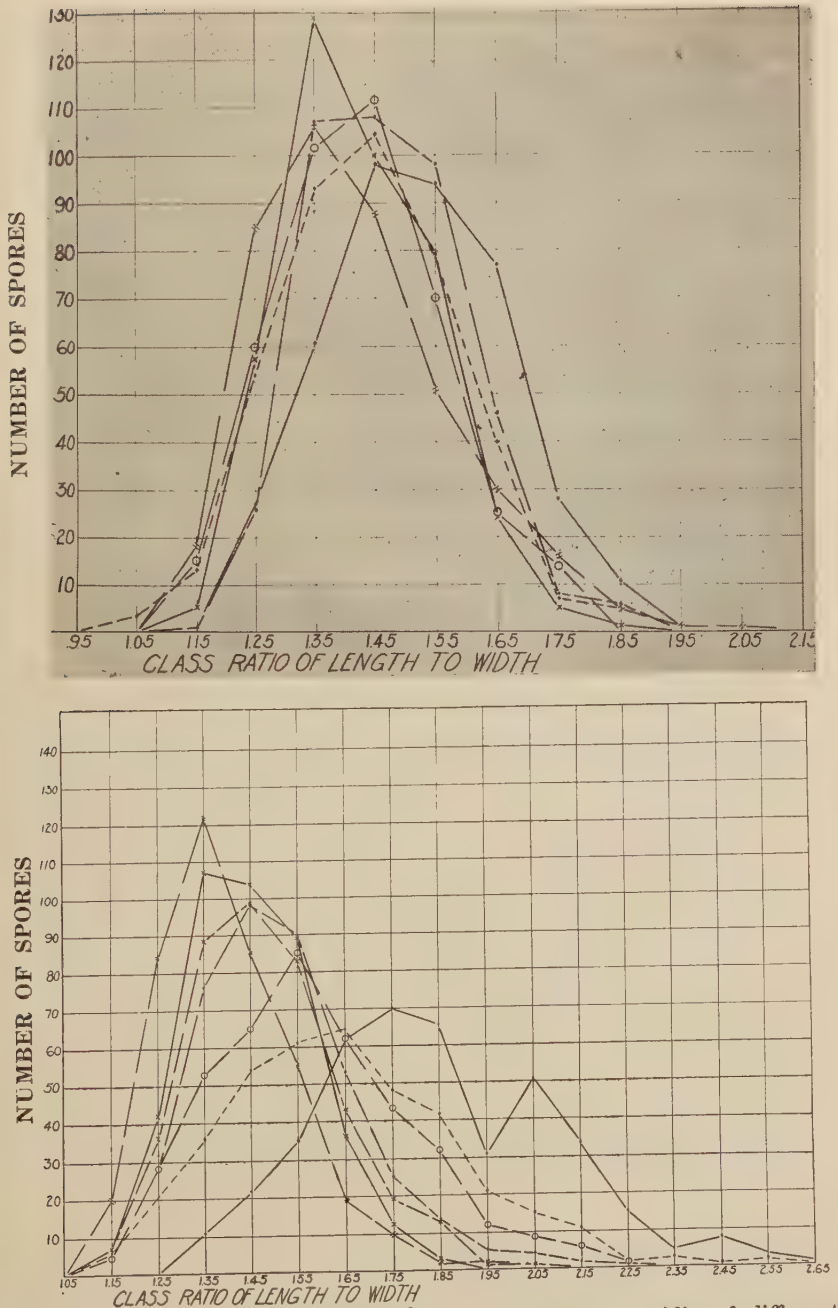

Fig. 46.—Differences in ratio of lengths to widths of conidia of different strains when grown on potato dextrose agar (above) and on oatmeal agar (below) under uniform cultural conditions. o— —o, strain 8I; .- - -., strain 8K; .— — —., strain 8L; x——x, strain 8M; x— — — —x., strain 8N; .——., strain 8P; 1:1— —1:1; strain 8Q.

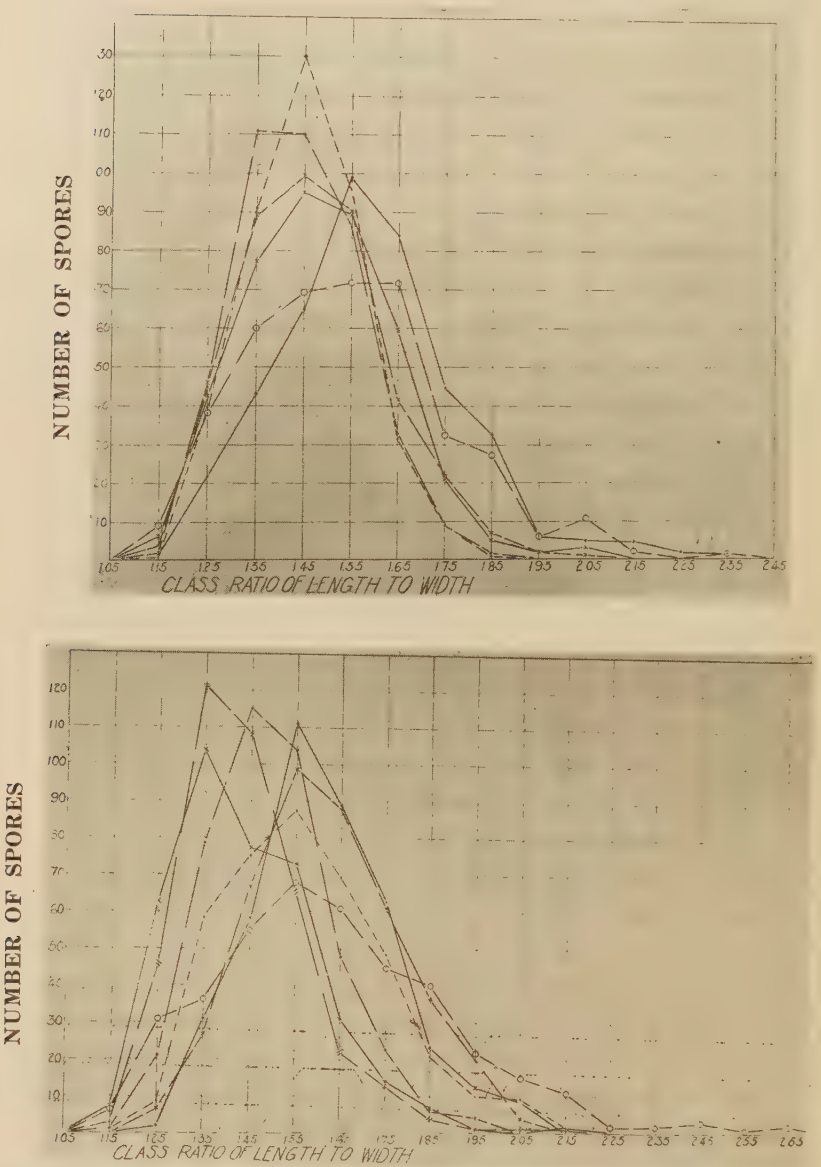

Fig. 47.—Differences in ratio of lengths to widths of conidia of different strains when grown on corn meal agar (above) and on corn meal flour (below) under uniform cultural conditions. o— —o, strain 8I; . - - -., strain 8K; .— — —., strain 8L; x——x, strain 8M; x— — —x, strain 8N; .——., strain 8P; 1:1;— —1:1; strain 8Q.

grown on potato dextrose agar and corn meal flour respectively. Rosenbaum *(29)* found *P. parasitica* had a mean ratio of conidial length to width of 1.75, but Dastur *(12)* found a ratio of 1.37, and Ashby *(2)* found a sporangial ratio of 1.32-1.40. The present study shows that these divergencies in shape, as those in size, are evidently influenced by substratum upon which the organism was grown, while the difference in physiologic specialization is in itself sufficient to account for such differences.

PATHOGENICITY OF THE VARIOUS ORGANISMS

Inoculation experiments were made in the greenhouse, using potted plants from three to six years old. As moisture is a very important factor in the development of the disease, the experiments were conducted in two series: A, in which the soil was kept near saturation by placing the potted plants in tubs and by keeping the outer tub partially filled with water to regulate the water level in the soil; B, in which the plants were watered frequently to keep them in good growing condition. In each series of inoculations, five plants were inoculated with each organism and eight checks were inoculated with sterile distilled water. Two methods of inoculation were used. In the first method the outer leaves were removed and the buds punctured with a "seeker" or "probe" which tapered from a sharp point to a diameter of 3/16 inch. On account of the small size of the needle, mechanical injury was reduced to a minimum. The point of inoculation was covered with sterile cotton and kept moist by wetting each day with sterile distilled water.

In the second method the plants were inoculated by pouring spores suspended in sterile water into the bud.

The incubation period varied from three to 10 weeks, that for plants inoculated by the first method being from three to six weeks and that for those inoculated by the second being from four to 10 weeks. Final notes were taken 90 days after inoculation. (See Table IX.) The highest percentage of plants were killed in the wet series inoculated with a needle; the next largest percentage in the dry series inoculated with a needle; the next largest in the wet series inoculated by pouring the suspension of spores into the bud, and the lowest percentage was in the dry series inoculated in the same manner. The most common symptom was spotting of the leaves. Plants inoculated by both meth-

TABLE IX.—The Results of Inoculating Coconut Seedlings, in (Series A) Soil Kept Nearly Saturated and in (Series B) Soil Kept Moist, with Various Strains of *Phytophthora*.

Strains of Phytophthoras	Method of Inoculation	Series A				Series B			
		No. Plants	No. Killed	No. Spott'd	No. He'thy	No. Plants	No. Killed	No. Spott'd	No. He'thy
120 (8I) —*P. faberi* from Florida	Sprayed					5	1	2	2
120 (8I) —*P. faberi* from Florida	Punctured					5	2	3	0
191 (119)—*P. faberi* from Florida	Sprayed					5	0	2	3
119 (119)—*P. faberi* from Florida	Punctured					5	1	4	0
8K—*P. faberi from* Philippines	Punctured	5	5						
8I—*P. faberi* from Florida	Punctured	5	4	1					
8L—*P. palmivora* from Porto Rico	Punctured					5	3	2	
119—*P. faberi* from Florida	Punctured					5	2	3	
8K—*P. faberi* from Philippines	Sprayed					5	2	1	3
8I—*P. faberi* from Florida	Sprayed					5	1	2	2
8L—*P. palmivora* from Porto Rico	Sprayed					5	0	3	2
119—*P. faberi* from Florida	Sprayed					5	1	1	3
8M—*P. faberi* from Jamaica	Punctured	5	5						
8I—*P. faberi* from Florida	Punctured	5	4	1					
8L—*P. palmivora* from Porto Rico	Punctured					5	2	2	1
8K—*P. faberi* from Philippines	Punctured					5	3	2	0
8N—*P. palmivora* from India	Punctured					5	2	2	1
8X (8I)—*P. faberi* from Florida	Punctured					5	4	1	0
8Q—*P. terrestris* from Florida	Punctured					5	3	2	0
8P—*P. palmivora* from Jamaica	Punctured					5	3	2	0
8Q—*P. terrestris* from Florida	Sprayed	5	2	1	2	5	1	1	3
8P—*P. palmivora* from Jamaica	Sprayed	5	3	1	2	5	1	1	3
8M—*P. faberi* from Jamaica	Sprayed					5	0	2	3
8M—*P. faberi* from Jamaica	Punctured					5	3	2	0
8N—*P. palmivora* from India	Punctured					5	2	3	0
8N—*P. palmivora* from India	Sprayed					5	0	3	2
8Q—*P. terrestris* from Florida	Sprayed	5	0	1	4				
8Q—*P. terrestris* from Florida	Punctured					5	3	2	0
8Q—*P. terrestris* from Florida	Punctured	5	5						
8Q—*P. terrestris* from Florida	Sprayed					5	1	2	2
8N—*P. palmivora* from India	Punctured					5	3	2	0
8N—*P. palmivora* from India	Sprayed					5		3	2
8A (8I)—*P. terrestris* from Florida	Punctured					5	1	3	1
8A (8I)—*P. terrestris* from Florida	Sprayed					5	0	2	3

ods developed this symptom, but it was more common in the plants inoculated by the second method.

Sixty percent of the spotted plants in series A died, while only 17 percent of those in series B succumbed. It is quite likely that still more of the plants would have died if they had been kept under observation longer.

It is evident from these experiments that moisture favors the development of the disease and that puncturing the bud also is conducive both to a more rapid development of the disease and to a more serious final result.

The original organism with which the plant had been inoculated was recovered from plants showing the early symptoms, in each series inoculated. In many cases pure cultures were obtained on plating out. In no case was it impossible to recover the original organism.

It was perfectly evident from the results of the inoculations that there were no essential differences in the pathogenicity of the various *Phytophthoras* used. This together with the results of the physiological and morphological studies, forces one to the conclusion that there is insufficient justification for considering *P. faberi, P. palmivora* and *P. terrestris* as separate species, even with the absence of the oospores.

LIFE HISTORY OF THE CAUSAL ORGANISM

SOURCE OF INOCULUM

Conidia are seldom found on specimens collected in the field, but are often produced on specimens incubated in moist chambers in the laboratory if the specimen is not overrun with other fungi and bacteria. Conidia are found on the leaf spots rarely, but they may be produced here also, if the specimen is placed in a moist chamber. On specimens collected in flooded fields, or soon after or during a series of rains, the conidia are abundant on the leaves and on the unfolded leaf of the bud. Moisture is a prerequisite for the development of spores. Clearly, therefore, there is an abundant source of inoculum.

Chlamydospores are frequently found in the mycelial felt on fleshy specimens, as well as in the diseased tissues, with the exception of leaf spotted tissue, where they are rare. Chlamydospores retain their vitality for a long time, as it has been found that the organism could be isolated from a diseased specimen held in the greenhouse for nine months after it had been killed

by the organism, or for 10 months after it had been inoculated.

It is evident that the conidia which are produced in moist weather may be a source of infective material. Chlamydospores formed in decaying bud rotted plants left in the field may also serve as inoculum. It is also possible that the organism may live in old plant parts left in the soil. Sherbakoff *(32)* has shown this to be the case with *P. terrestris,* which attacks tomato.

DISSEMINATION OF THE FUNGUS

Evidence from field observations indicates that the spores are carried by the wind, wind blown rain, and water. Wind undoubtedly aids in the distribution of the spores of this *Phytophthora as* well as those of other species of the same genus. Weston *(40)* has clearly shown the role that wind and wind blown rain play in the dispersal of the spores of the Philippine Sclerospores, while Butler *(8)* has shown that wind and wind blown rain spread *P. palmivora* in the Palmyra palm. Coleman *(10),* Tucker *(26),* Ashby *(2),* Reinking *(28)* and others have pointed out similar cases of *Phytophthora* spread.

There are a number of coconut nurseries in the peat soils along the inland waterways in southeastern Florida, between Palm Beach and Miami. In one of these nurseries at Palm Beach many specimens of diseased palms were removed at various times, and it was not more than six months from the date of the first finding until bud rotted palms had been collected from every nursery south of Palm Beach along this waterway. It so happens that this canal frequently floods these nurseries and thus offers one explanation as to the dissemination of this *Phytophthora.* There is no doubt that water carries the spores to the bud from the leaf surfaces where they have lodged. A palm plant is constructed in such a manner that the upright leaves conduct water falling on them to the crown of the plant.

Diseased nursery stock is also instrumental in spreading the disease and it was not unusual to trace the source of an infection to diseased stock.

Cultivation of the plants plays a minor role in the spread of the disease, as this practice is followed only during dry weather. Dipterous insects may play a role in spreading the pathogene, as a little scavenger fly and its larvae are found constantly associated with the diseased plants. Leach *(19a)* has found a species of this insect to be not only a carrier of the potato black-

leg organism, but an agent of inoculation as well. Borers, cockroaches and other insects are found in or on the plants, but the little scavenger fly seems to be more definitely incriminated.

LONGEVITY OF SPORES

Chlamydospores, sporangia, and zoospores retain their viability only a very short time if they are permitted to dry. The life of any of the spore forms is prolonged if they are kept under slightly moist conditions. Temperature also may be a factor, as it has been noted that cultures left at room temperature (22-26°C.) from two to three months lose their viability. Cultures held at 16-18°C. in the ice box for the above period retain their vitality. Chlamydospores germinate readily and even an occasional sporangia germinates. In case zoospores do not germinate in a few hours after forming, it seems that their power to germinate is lost. Undoubtedly the chlamydospores are the most important in enabling the organism to persist through adverse conditions. They have been found to retain their vitality in agar culture for more than a year, and in bud rotted specimens held in moist conditions in the greenhouse for more than nine months.

SPORE GERMINATION

CONIDIA

Conidia are potential zoosporangia, and consequently may germinate by the production of one or more germ tubes or by the production of zoospores. The manner of germination seems to depend upon certain environmental conditions which have not yet been definitely determined. If the conidia are placed in culture media, they send out from one to six germ tubes. In case one or two germ tubes are formed, these appear near the papilla, and, in case more are formed, they appear at any point on the spore. Frequently a primary conidium may give rise to a secondary conidium, a secondary conidium to a tertiary conidium, etc., until the organism exhausts itself. Each of these succeeding spores becomes smaller and smaller; but yet, like the original spores, each may act as a sporangium. Occasionally a conidium gives rise to a chlamydospore-like body which germinates by zoospores. In this case a zoospore may germinate in situ or escape through a rupture in the spore wall. (See Fig. 48.)

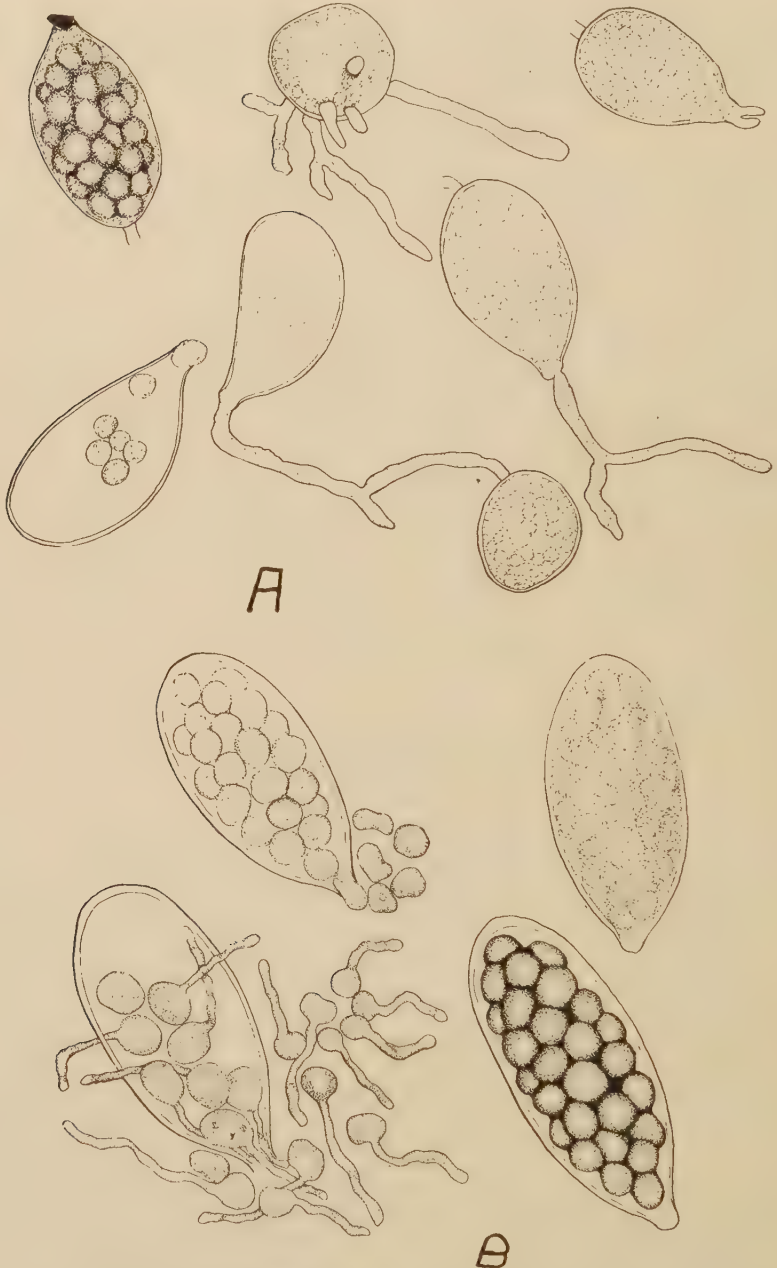

Fig. 48.—Types of spore germination. A. Chlamydospores by direct germination, conidia by direct germination, zoosporangia by zoospore formation (x 500). B. Showing successive steps in zoospore formation, liberation and germination of zoospores (x 750).

In the case of zoospore formation, from five to 30 zoospores may be produced. The size of the sporangium is the limiting factor, as the zoospores are from 7μ to 11μ in size. They are formed as irregular bodies within the sporangium, and sometimes they do not round up until they are liberated. In other cases they may be formed as irregular bodies within the sporangium, where they round up and take on the general appearance of a bunch of grapes. Before they are liberated from the sporangium an aggregation takes place. Then the zoospores move rapidly around the walls of the sporangium, all moving in the same direction. During this process the papilla dissolves and the zoospores escape by means of a considerable elongation of themselves. The rotary movement continues until all the zoospores are free or settle down within the sporangium. Once a zoospore escapes from the sporangium, it remains motionless for a few seconds at the mouth of the papilla. Sometimes a number of these spores cluster together before they swim away. The zoospore then becomes reniform, is greenish in color, contains one or more vacuoles and the cilia appear on the ventral side. By means of these cilia the zoospores swim rapidly, at first in a zigzag course, but gradually they become motionless and round up. If the spore hits an object in the course of its travel, it bounces off and then goes forward or retraces its original path. After coming to rest the zoospore germinates within two hours by sending out a germ tube. Zoospores which are not liberated from the sporangium may germinate in situ and send the germ tubes through the sporangial wall.

Butler *(8)* found that *Phytophthora (Pythium) palmivora* liberates its zoospore mass into a bladder, or prosporangium, in which the zoospores are differentiated while in other cases the zoospores are liberated directly from the sporangium. Dastur *(12)* finds that a prosporangium is formed in the case of *P. parasitica,* and Rosenbaum *(29)* reports this bladder-like body in the case of *P. cactorum, P. omnivora (P. arecae)* and *P. parasitica.* Ashby *(2)* failed to note this method of zoospore liberation in his studies of *P. palmivora* in Jamaica, while Reinking *(28)* and Gadd *(15* and *16)* observed direct liberation of the zoospore from sporangia of *P. faberi.*

In making a study of spore germination, it has been found that young spores germinate by zoospore formation more rapidly than old spores. The highest percentage of zoospore forma-

tion was noted in water condensed on the walls of a test tube in which a culture of strain 8L was growing on lima bean agar at a temperature of 27°C. (Fig. 49.)

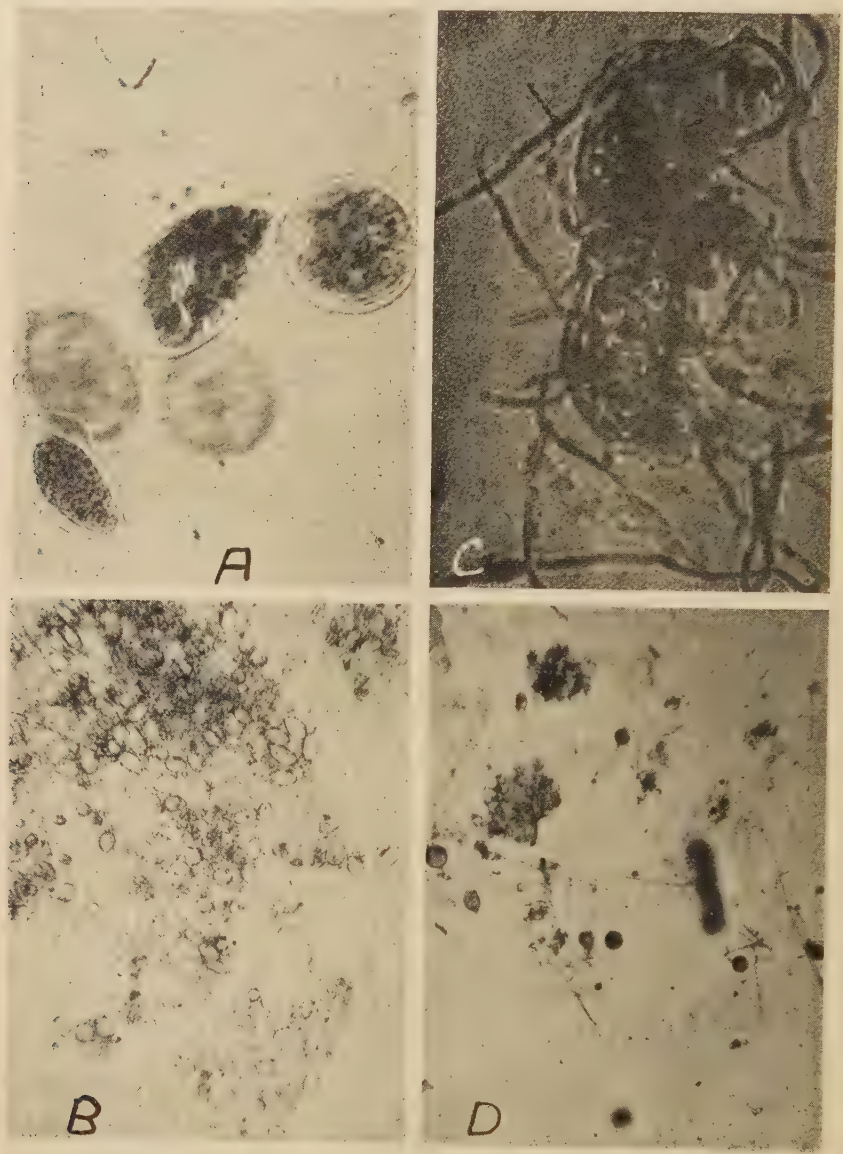

Fig. 49.—Zoospore production showing various stages of development and germination. A. Sporangia about to liberate zoospores (x 500). B. Numerous zoospores and empty sporangia (x 90). C. Zoospores germinating in place within a sporangia (x 500). D. Zoospores germinating (x 90).

Spores placed in distilled water germinated very poorly regardless of age or the treatment. Placing spores in tap water, rain water, water collected from the host, or water in which a little host tissue had been added, is conducive to a high percentage of conidia germinating as zoosporangia. This is especially true for strains 8L and 8K, when chilled in the icebox in a water suspension containing macerated host tissues, where as many as 80 percent of the spores germinated as sporangia. Zoospore formation could be noted after 15 minutes of chilling and would continue for approximately two hours. The remaining ungerminated spores would then act as true conidia and germinate by germ tube formation.

Ward *(39)* considered that the liberation of zoospores was favored by the presence of free oxygen. Melhus *(24)* concluded that there was sufficient oxygen in the conidium of *Phytophthora infestans* to permit germination without the presence of free oxygen in water. He also concluded that temperatures between 11-20°C. are conducive to zoospore formation. Coleman *(10)* thought that light was essential for formation of zoospores by *P. omnivora* var. *arecae*. Gadd *(16)* showed that light, aeration of water and temperature are all important for zoospore formation in *P. parasitica* and *P. omnivora* var. *arecae* but light is unessential in the case of *P. faberi*. Reinking *(28)* found zoospore formation in sporangia that had been freshly formed on old cultures. Tucker *(36)* noted only an occasional empty zoosporangium and states that the spores germinate primarily by germ tube formation. Uppal *(38)* concludes that direct and indirect germination are two different phenomena, the former being a type of growth, while the latter is a mere breaking up of the protoplasm into independent units. He also finds that under proper temperature conditions neither air nor oxygen are essential for zoospore formation.

CHLAMYDOSPORES

Chlamydospores will germinate readily within 12 to 24 hours in water or in culture media. They usually produce several germ tubes, which may appear at any point on the spore. Chlamydospores have not been found to produce conidia upon germination nor to germinate as sporangia, yet chlamydospore-like bodies produced from sporangia have been seen to germinate as spor-

angia. Chlamydospores frequently become vacuolate and apparently break up into large granules which look like zoospores, but which have not been definitely identified as such.

METHOD OF INFECTION

By just what method the organism enters the host has not been satisfactorily proven. Lateral penetration of the bud tissues has been proven to take place in inoculation experiments, and, from the symptoms of the disease, this method appears to be the more common type. Vertical penetration may occur according to field observations. Specimens have been collected that show no signs of leaf spotting or leaf blighting to indicate lateral penetration. In the inoculation experiments conducted in the greenhouse this method was employed without success. Repeated experiments have been made to determine whether the organism entered the host through stomata or directly through the epidermis, but the results were inconclusive. Coleman *(10)* states that germinating zoospores form a type of appresorium at the end of the germ tube which enters the host through the stomata.

There is direct and observational evidence that the pathogene penetrates the sheathes of the older leaves and then pushes its way into the younger tissues. The organism may also get into the bud from above by spores lodging in the funnel-like area formed by the sheathes of the older leaves around the bud. Usually this sheath funnel is partly filled with water, in which the spores germinate. The organism attacks the young leaf, producing lesions which later appear as a series of spots across the pinnae of the leaf. (See Fig. 50.) Frequently the organism finds its way to the primordal bud tissues, which it rapidly destroys.

PATHOLOGICAL ANATOMY

The mycelium is always inter-cellular. It never has been observed to penetrate into the cells but sends finger-like haustoria into them. The mycelium ramifies in the inter-cellular spaces and grows much more rapidly in a vertical direction than laterally. The generative tissues seem to be the most susceptible and are destroyed very rapidly. The mycelium extends vertically in both directions, but it does not progress far downward be-

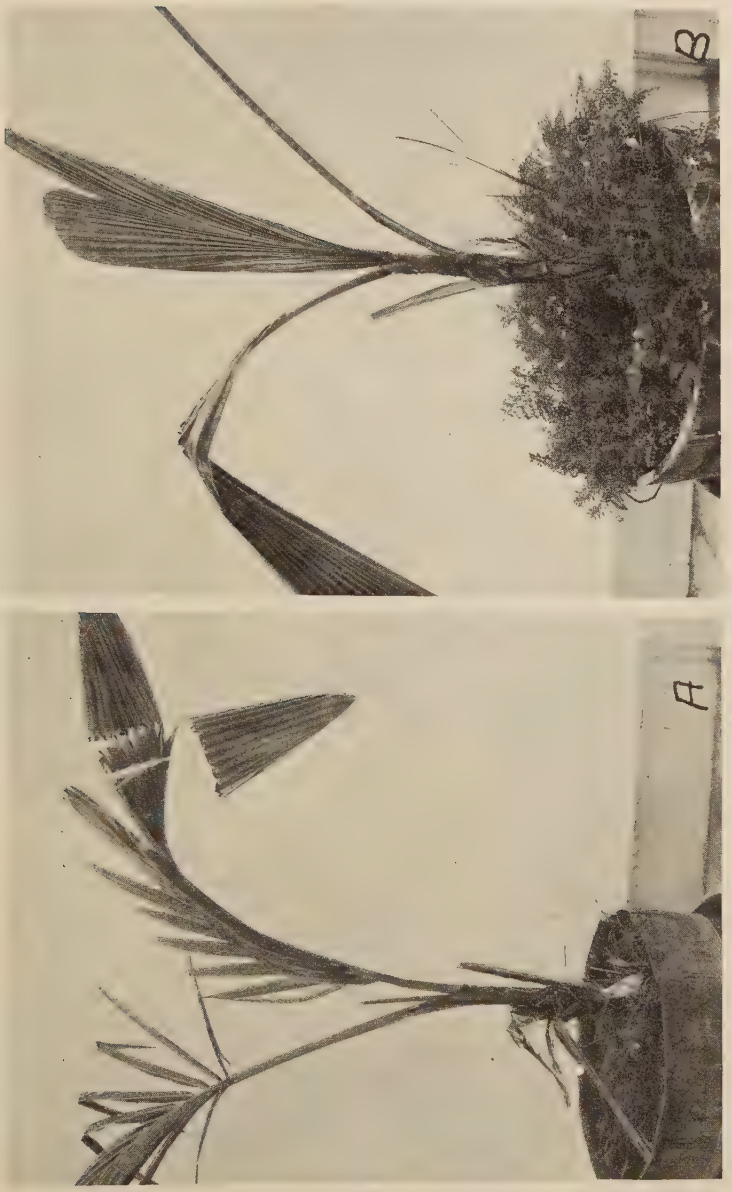

Fig. 50.—Three-year-old plants inoculated and held in greenhouse. A. Shows a type of leaf injury noted in inoculated plants. B. Bud of plant completely destroyed.

cause it soon reaches mature tissues which retard its growth. The mycelium grows rapidly upward until it has reached the level of the water retained in the bud and then the rate of growth becomes slower. The hyphae may grow upward from six to 18 inches, depending upon the size of the host plant and upon the succulence of the tissues.

The inter-cellular spaces are ramified with mycelium, and the middle lamella appears to be dissolved by the organism. In advanced cases of the disease many unattached cells may be found in a microscopic mount. These free cells are plasmolized and are frequently destroyed by saprophytic fungi and bacteria. Thus, the combined action of the parasitic *Phytophthora* and saprophytic organisms promptly reduces the primordal tissues to a gelatinous mass.

SEASONAL DEVELOPMENT OF THE DISEASE

There is no particular time of the year during which the disease is most prevalent. Temperature is not a limiting factor in the development of the disease in Florida, as the optimum temperature for the organism is near the daily mean temperature for Florida.

It also happens that the organism has a lower minimum and higher maximum for growth than the daily minimum or daily maximum temperature for any given period of the year. Moisture apparently is the all important factor, as the disease is more prevalent in the lowest peat soils and in the crowded nursery plantings where moisture is most abundant. Invariably, sporadic outbreaks of the disease occur within a few months after rainy periods. (See Fig. 51.)

The exceptionally large number of findings in the months of March, April and May, in 1925, is due to the fact that the first survey of the infested area was being made, as well as to the very heavy precipitation of approximately 25 inches during October, 1924. There is a very definite correlation shown between the curves giving the rainfall and the bud rot findings from May, 1925 to May, 1927. Butler *(8)* and McRae *(23)* have reported similar conditions as affecting the bud rot outbreaks in the Palmyra palm in India. Coleman *(10)* reports similar conditions for outbreaks of bud rot of the Areca palm. Reinking *(27)*, Tucker *(36)*, and Ashby *(2)* have noted seasonal influ-

ences upon outbreaks of coconut bud rot in the Philippines, Porto Rico, and Jamaica, respectively.

Plants growing in low peat soils have suffered heavily from the ravages of this disease in Florida. In the vicinity of Palm Beach, low lands that were planted to coconuts were filled in by pumping soil from the bay. The land was flooded with mud and water, and, under such conditions, bud rot could be found in these plantings for months; even though the diseased plants were destroyed as rapidly as found.

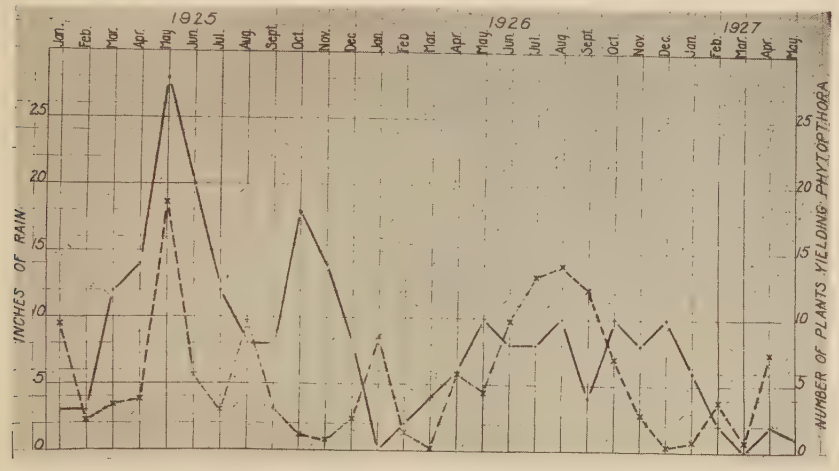

Fig. 51.—Curves showing the relation of rainfall and the occurrence of bud rot, Jan. 1925-May 1927. Rainfall in inches .——. Bud rot specimens x— —x.

CONTROL

In general, the methods of control used are exclusion, eradication, and protection. All importation of nuts and plants from foreign territories for propagation is prohibited.

Local quarantines are placed on all properties when coconut bud rot is found on them, as well as on properties within a quarter-mile zone of the infected property. This quarantine is effective for six months after the last finding of the disease. During this time six monthly inspections are made, and, in case no newly infected plants are found, the quarantine may be lifted.

When diseased plants are found they are immediately removed and burned. In addition, the plants in the vicinity of an infected plant are sprayed with 5-5-50 Bordeaux mixture plus a sticker of fish oil soap.

The above methods of control have proved effective, as shown by the decreasing number of diseased plants (Fig. 51). The task of freeing properties of bud rot has proven to be comparatively simple, except in those plantings located in areas especially favorable to the development of the disease. Of the fifty odd infected properties handled by the above method, only a few have come under quarantine a second time. The employment of these control measures by the nursery inspectors, in cooperation with the growers, will undoubtedly hold the disease in check, but never completely eradicate it.[6]

DISCUSSION

The results of the present study show that there are only minor differences in the physiology and morphology of the different strains and so-called species of *Phytophthora* investigated. There were no differences in the pathogenicity on coconut.

There is considerable variation in the physiological characteristics of all the different *Phytophthoras* investigated. The rate of growth, the production of submerged and aerial mycelium, and the types of spore forms produced vary on different media. There may be practically no differences between different strains on certain media, while on others they may differ from each other considerably. However, variations within any given strain are as great as or greater than variations between the different strains or so-called species. It is very doubtful, therefore, whether one could always distinguish between the different so-called species and strains, even when growing on the same media.

The morphological characters of the different strains are quite similar and do not vary as much as the physiological characters. Neither is there as great variability in the morphology of a given strain as there is in the physiology. The methods of spore production of the different strains are identical, as are the methods of spore germination. The size of the spores is the most variable of all the morphological characters, but there are not always significant differences in the spore sizes of dif-

[6]Subsequent to the time this was written, the Plant Board modified to a great degree its policy with respect to the coconut bud rot situation, it having become evident as the result of more extended investigation in both field and laboratory that the relatively drastic measures outlined in the text could be considerably lessened without materially lessening protection against further spread.

ferent strains grown on the same medium and under identical conditions. There is as much variation in the spore size of any given strain grown on different media as there is between different strains when grown on the same media. It seems very doubtful, therefore, whether there is any justification for considering the different organisms as distinct species. It seems much more reasonable to consider them merely as physiologic forms.

Leonian *(20)*, working primarily on the physiology in the genus *Phytophthora*, also concludes that all the organisms dealt with in this paper belong to the same species, which he calls *P. omnivora* DeBary, and in which there are numerous strains. These strains he finds may be grouped into two sub-groups; the one including *P. terrestris* and *P. parasitica*, while the other embraces *P. palmivora* and *P. faberi*.

It has been suggested that the only safe criteria for the determination of species in the genus *Phytophthora* are the size and characters of the sexual bodies. If this be true, there are so-called species that have no sufficiently distinct characters to entitle them to specific rank. Some of the *Phytophthoras* were raised to specific rank long before their oospores were found, and even to date, many of these organisms do not produce oospores in pure cultures. Of the group under consideration, those that yield oospores produce them in a similar manner. The small variability in their morphological and physiological characters as well as their common host range leads one to conclude that their specific rank is not justifiable. Leonian *(20)* has placed these organisms into a group species, *Phytophthora omnivora* DeBary, and the writer sees no good reason for not agreeing with this disposition of so-called species which resemble each other so closely.

All of the numerous workers who have studied the so-called species discussed in this paper agree that there are only minor morphological and physiological differences. This would seem to confirm still further the opinion of the writer, and of Leonian, that the *Phytophthoras* causing bud rot should be included in one group species. Not only are these organisms very similar physiologically and morphologically, but their pathogenicity for coconut is the same.

Ashby *(1)*, Shaw & Sundararaman *(31)*, Sundararaman *(35)*, McRae *(23)*, and Tucker *(36)*, have shown that *P. palmivora*

Butler will attack the coconut plant causing bud rot. Tucker *(37)* finds that *Sabal causarium* (Cook) Beccari is also attacked by *P. palmivora.* Reinking *(28)* has proven that *P. faberi* Maubl. attacks the coconut palm, and the writer has shown that *P. terrestris* Sherbak. also causes bud rot. Ashby *(2)* has shown that *P. parasitica* causes a leaf stalk rot as well as bud rot of the coconut. He also agrees with Dastur *(12)* that it is synonymous with *P. terrestris* Sherbak., which, in Florida, causes a fruit rot of the tomato and a root rot of citrus. Reinking *(28)* was successful in producing fruit rots of tomato, apple, papaw, and cacao; as well as a seedling blight in a number of plants with *P. faberi.* Gadd *(15),* from a study of strains of *P. faberi,* isolated from various diseased plants, concludes that the various organisms may be separated into two groups, which he concludes are biological varieties.

SUMMARY

1. Coconut bud rot, caused by a species of *Phytophthora,* was found in the vicinity of Miami in January, 1924, and, since that date, has been found in an area 140 miles along the southeastern coast of Florida.

2. There are some 2,250,000 coconut palms in Florida, having a commercial value of approximately $3,000,000. To date 75,000 bud rotted plants have been destroyed.

3. The most noticeable symptoms of the bud rot are yellowing, wilting, and death of the terminal bud, which eventually falls from the plant, followed by the dying of the outer leaves. The generative bud tissues are reduced to an odoriferous gelatinous mass from which numerous saprophytic organisms may be isolated.

4. Several species of *Phytophthora* have been described as the causative agents of coconut bud rot, i.e. *P. palmivora* Butler, *P. faberi* Maubl., *P. parasitica* Dastur, *P. terrestris* Sherbak. and *P. omnivora* var. *arecae* Colem.

5. Strains of *Phytophthora* isolated from bud-rotted palms in Florida have been compared in their physiology, morphology and pathogenicity with *P. terrestris, P. faberi,* and *P. palmivora.* These latter organisms had been isolated from various plants by several workers in different countries.

6. Differences were noted in reactions of the various organisms to different temperatures and media; in quantity and char-

acter of vegetative mycelium, as well as in the number of spores produced.

7. All the strains studied produced conidia and chlamydospores in the same manner, but in no case was the production of oospores observed.

8. Statistical studies of spore morphology were made under comparable conditions, the various organisms having been grown on similar media under uniform cultural conditions. Data were obtained on length, width and shape of conidia, and the diameter of chlamydospores.

9. By the use of biometric constants the organisms studied were compared when grown on the same or different media. The organisms differed significantly from one another when grown on the same media under uniform environmental conditions. However, each organism varied considerably when grown on different media. It is apparent that the variation within the same organism grown on different media is as great as or even greater than the variation between different organisms grown on the same media.. Different culture media affected spore size of the different strains differently.

10. The ratio of length to width of the conidia has been determined in order to establish the composite shape of the spores. There was great variability, both intrinsic as well as caused by the medium upon which the organism was grown.

11. Wounded and unwounded plants were inoculated with each organism and bud rot was readily produced. The percentage of successful infections was much higher in the wounded plants. Plants grown in very moist soil succumbed more readily to the disease. There were no distinguishable differences in the disease symptoms produced by the different organisms.

12. The mycelium within the host tissue is inter-cellular, ramifies in the inter-cellular spaces, and sends finger-like haustoria into the host cells. Very little progress is made by the mycelium below the generative tissues into or up the bud above where it projects from the sheath.

13. Conidia are seldom, if ever, produced on diseased plant parts unless there is an abundance of moisture, but chlamydospores are frequently found in the mycelial felt on the diseased parts of the plant.

14. Bud-rot-producing *Phytophthora* spread by means of conidia, by the aid of wind, wind-blown rain, and by water,

during the rainy season. Chlamydospores, and even bits of mycelium, are possibly carried by the same means, and even by the scavenger flies.

15. Each conidium is a potential sporangium and may germinate by means of a germ tube or by producing zoospores. Chlamydospores germinate by the production of one or several germ tubes.

16. Just how the pathogene gains entrance into the plant has not been determined. but direct penetration of the organism into the bud tissues, either laterally or vertically, is probable.

17. Conidia and zoospores have a short period of life, even under the most favorable conditions, and chlamydospores seem to be the only means of tiding the organism over adverse conditions. Chlamydospores have been found to retain their vitality in diseased plant parts for nine months.

18. Coconut bud rot may appear at any time of the year, but is found more commonly a month or two after periods of heavy rains. The disease takes its greatest toll of plants in nurseries, particularly on low peat soils.

19. From morphological, physiological and pathological studies of the several organisms causing coconut bud rot only minor differences have been noted. These differences are not sufficiently great to warrant the classification of these organisms as species, but, on the other hand, they seem to be only physiologic strains within a species. The writer, therefore, agrees with Leonian in placing all these strains in the group species *Phytophthora omnivora* DeBary.

20. Control has been effected by the use of local quarantines, destruction of diseased plants, and the protection of the healthy plants by the use of Bordeaux mixture and fish oil soap.

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VITA

The author, James Lewis Seal, was born in Greenwood, S. C., on January 25, 1893. He was graduated from the Quarry (Iowa) High School in 1909. He received the B.A. in Agriculture from Clemson College in June, 1913 and the M.S. from Iowa State College in 1916 with a major in Botany. He entered the Graduate School of the University of Minnesota in October, 1920 and received the degree of Doctor of Philosophy in September, 1927. He served as an Instructor in the Plant Pathology Department, University of Minnesota from 1920-1927. He is at present Associate Plant Pathologist at the Polytechnic Institute, Auburn, Alabama.

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